SEEDBED MICRO-SITES AND THEIR ROLE IN POST-FIRE SUCCESSION OF THE LICHEN-BLACK SPRUCE WOODLAND IN TERRA NOVA NATIONAL PARK, NEWFOUNDLAND

RANDAL GERARD POWER

Seedbed micro-sites and their role in post-fire succession of the lichen-black spruce woodland in Terra Nova National Park, Newfoundland

by

© Randal Gerard Power

A thesis submitted to the

School of Graduate Studies

in partial fulfilment of the

requirements for the degree of

Master of Science

Department of Biology
Memorial University of Newfoundland

September 2005

St. John's Newfoundland

ABSTRACT

Effects of a recent wildfire in the lichen-black spruce woodland in Terra Nova National Park, Newfoundland, were investigated to determine the interaction between fire intensity and fire severity; plus effects on forest-floor disturbance, on canopy seed banks, and on black spruce regeneration. As there was much exposed mineral soil from ant activity on this site, the potential for enhanced post-fire black spruce recruitment due to ants was also investigated. A seeding trial considered four potential seedbeds available: areas of high severity; areas of low severity; active ant nests; and abandoned ant nests. In addition, the amount and distribution of seed rain in the burned area was measured in an attempt to assess factors that affect the pattern and success of black spruce recruitment following fire. Duff depths were reduced by fire by as much as 50% while lichen depth by up to 88%. Ant nests occurred at a density of 6.15 per 100m² in the burned areas compared to 2 per 100m² in the unburned forest. Black spruce seed-fall, while low at 16 539 seeds per ha in the year following the fire, was sufficient for re-establishing the low-density lichen woodland community at an initial density of 524 seedlings per ha by 2003. However, a mean cone removal of 52% by non-native red squirrels may be limiting the establishment of a higher-density forest. Available seedbed was limited by the extensive caribou-lichen mat, but over 40% of successful black spruce seedlings in the seeding trial germinated in this substrate, compared with 33% for inactive ant nests and 26% for high severity burn. Seedlings were most likely to become established and survive in desiccation fractures in the lichen mat. The presence of abandoned ant nests did result in germination, but did not necessarily result in establishment as seedling survival was reduced from 89% to 44% after winter. Seedling mortality on scorched organic soil substrate under former spruce canopies was highest at 71%. Active ant nests produced no germinants in the trial and were the least suitable for germination. Drier and warmer than normal conditions in 2003, resulting in soil moisture deficits, appeared to be the main limiting factor for black spruce germination and survival. The next several years will be critical for subsequent black spruce germination and survival and in determining if re-establishment of the recently burned lichen woodland in TNNP will be successful.

Key Words: Ants, black spruce, boreal forest, fire severity, lichen woodland, seedbed, seen rain, wildfire

ACKNOWLEDGMENTS

First of all, I want to thank my supervisor, Dr. Luise Hermanutz and committee members Dr. Brian McLaren and Dr. Edward (Ted) Miller for their continued support over the long life of this research project. I appreciate your patience and for sticking with me. Also, thanks are due to my former supervisors Renee Wissink and Peter Deering who supported me in my M.Sc. quest. Allowing me to juggle job and education made this possible. I thank Mr. Blair Pardy for moral support in the marathon towards completion. I am especially grateful to Parks Canada for supporting my educational and professional development.

As for help in the field, I'd like to extend special gratitude to Mr. Kirby Tulk, who provided incalculable assistance. His organization, readiness and thoughtfulness made for organized field trips and data collection. Without him this project would not have succeeded. Rod Cox helped build and deploy the seed traps and assisted with field data collection. Additional field helpers were Cheryl Ryan, Melanie Chaulk, Sherri Nash, Robin Bloom and Stephen Cunningham. Very special thanks are due to Mark Simpson and Mike Rose for their logistical and field help. I also thank co-workers David Cote and John Gosse for statistical discussions and Tracy Harvey for help with the maps.

I owe a debt of gratitude to my wife, Jewel Cunningham who had to endure many, many discussions about this project and who has been with me through it all. Lastly, I dedicate this paper to my son, Russell.

TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

Page

LIST OF FIGURES (Continued)

Page

CHAPTER 1: INTRODUCTION

1.1 BACKGROUND

The lichen-black spruce woodland, a forest type dominated by an extensive carpet of lichens (*Cladina* spp.), is a unique community occupying a small portion (1.3 km^2) of Terra Nova National Park (TNNP), Newfoundland. It is associated with dry, sandy soils and is a component of the northern boreal forest, existing from the Yukon to Newfoundland and Labrador, (Rowe, 1972). The location in TNNP is one of the most easterly and southerly sites known for the community and is at the perimeter of its range. This forest type is highly susceptible to wildfire (Viereck, 1973) and several authors have described the fire origin of the lichen woodland community (Treter, 1995; Alexander *et al.*, 1991; Morneau and Payette, 1989; Sirois and Payette, 1989; Dyrness *et al.*, 1986; Auclair, 1983; Kershaw, 1977; Rowe, *et al.*, 1975).

Fire is important to the development of lichen woodland. During wildfires, forest floor disturbance occurs through combustion of organic soil, or duff (Ryan, 2002; Foster, 1985; Heinselman, 1981). Forest floor disturbance is vital in providing suitable seedbeds for many boreal plant species, critical for successful seedling establishment and hence, boreal forest regeneration (Ryan, 2002; Nguyen-Xuan *et al.,* 2000; Greene *et al.,* 1999; Sirois, 1995; Treter, 1995; Foster, 1985), especially for black spruce (*Picea mariana* (Mill.) B.S.P.) (Bloom, 2002; Allan, 1997; Day, 1982; Zasada, 1979). Seedbed conditions for black spruce are generally improved by burning, as competing vegetation is destroyed and duff depth reduced, permitting the roots of germinating spruce to reach the relatively stable moisture conditions of mineral soil (Ryan, 2002; Foster, 1985; Kilgore, 1985; Day,

1982; Heinselman, 1981). As a result, seed germination and seedling survival for black spruce usually increase with increased fire severity, which is the degree and extent of combustion of the organic layer (Ryan, 2002; Herr and Duschene, 1995; Sirois, 1993; Day, 1982). It follows that in the lichen-black spruce woodland, the partial or complete removal of the lichen layer and forest floor during fire is important for stand regeneration (Bonan, 1989), as seedling recruitment is inhibited (Alexander *et al.*, 1991) and limited to cracks (openings created by desiccation) in the lichen mat (Sirois, 1993), especially in late stages of succession.

Nevertheless, fire behaviour is complex and may not always lead simply to stand replacement. In the lichen woodland, extensive high-severity fires creating spruce seedbeds are uncommon (Payette *et al.*, 2000; Sirois, 1995; Alexander *et al.*, 1991). This is primarily due to the low-density structure of the community and the insulating nature of the lichen layer. In areas unoccupied by black spruce trees, where the bulk density of lichens is low, insufficient heat is generated to burn away the full duff layer (Alexander *et al.*, 1991). In addition, the lichen layer is difficult to burn completely away due to the high amount of moisture at its base (Lafleur *et al.*, 2002; Sirois, 1993). Yet, localized areas of high-severity fire may occur under black spruce clumps, with the extent of severity dependent on clump density and distribution. Advancing flame results in torching of spruce trees and their bulk density produces greater heat. Thus, fires are more severe, more mineral soil may be exposed, and more seed germination and establishment may occur (Alexander *et al.*, 1991). Although fire behaviour would seem to improve conditions for establishment from seed, paradoxically, the massive destruction of the

canopy seed bank by intense crown fire is equally likely (Arseneault, 2001; Simard and Payette, 2001; Zasada *et al.*, 1979). Thus, it is difficult to predict the effects of wildfire on forest succession.

Other factors also contribute to the success or failure of tree regeneration. Non-native red squirrels (*Tamiasciurus hudsonicus*), which were introduced to the island of Newfoundland in the mid 1960s (Payne, 1976) are now found in most forested areas on the island and are abundant in TNNP, with recorded densities as high as 1 per hectare (Reynolds, 1997). They are important predators of cones and forest regeneration is adversely affected when squirrel densities are high. Squirrels were responsible for > 85% of cone predation in white pine (*Pinus strobus* L.) in Newfoundland (English, 1998) and have the potential to decimate conifer cone crops in poor seed years (West, 1989).

Another source of disturbance is by insects, particularly ants, which are abundant in terrestrial ecosystems worldwide (Hölldobler and Wilson, 1990). Ants affect soil structure and processes, directly and indirectly influencing the flow of material and energy in ecosystems and thus affecting the habitats of other species (Folgarait, 1998). Ants have been found to have effects on soil chemistry (Lenoir *et al.*, 2001), on boreal soil fauna (Laakso and Setälä 2000; Laakso, 1999) and on soil microbial activity (Dauber and Wolters, 1999). Enrichment of soil through ant activity is key to the development of vegetation (Medina and Silva, 1990; Sarmiento, 1984). Soil underlying ant nests provides more nutrients and enhanced microbial dynamics than surrounding soil (Lafleur, *et al.*, 2002), effects that may extend beyond the mound perimeter into the surrounding ecosystem (Nkem, *et al.,* 2000). In many locales, plant species composition and

abundance benefit from proximity to ant mounds (Folgarait, 1998; Hölldobler and Wilson, 1990). Thus, if ants are abundant in an ecosystem, their potential influence on the success or failure of tree germination must be taken into consideration.

The effects of ant nest mounds on soil chemistry and vegetation have been studied in other ecosystems (e.g. Andersen and Ashton, 1985; Culver and Beattie, 1983; King, 1977), but not extensively in the boreal forest, either alone or in combination with natural disturbance such as fire. In a review of ant biodiversity and its relationship to ecosystem functioning, Folgarait (1998) cites many studies carried out on ant biodiversity and its relationship to ecosystem functioning in Australia (8 studies), South America (7), the United States (6), Central America (3), Africa (2) and Europe (4), but few from high latitudes. Studies on boreal ants have been largely centred in Finland (Lenoir *et. al.*, 2001; Laakso and Setälä, 2000; Laakso, 1999). With the exception of one study in Quebec (Lafleur *et al.*, 2002) little detail is known about ecological roles of ants in lichen-black spruce woodland.

1.2 PROJECT RATIONALE, GOAL AND OBJECTIVES

On 13 June 2002, a wildfire started in TNNP, that spread in a westward direction at a rate of ~ 10 meters per minute, burning 98 hectares (ha), or approximately 80% of the lichen-black spruce forest. The fire was of mixed-intensity and the effect of the fire on both canopy seed banks and on forest floor disturbance and subsequently on black spruce regeneration was unknown. Additionally, large areas of exposed mineral soil occur on this site due to ant activity, which could potentially enhance black spruce

recruitment from seed. In order to understand post-fire recovery and structure of this forest type, it was important to analyse seed source, potential impact on seed source, forest floor disturbance and post-fire seedling survival in conjunction with fire severity.

Specifically, the project investigated black spruce seed germination and survival on four seedbeds; 1) the lichen mat; 2) scorched duff under burned black spruce clumps; and exposed mineral soil on 3) active ant nests and 4) abandoned ant nests. The main hypotheses were: a) black spruce regeneration through seed dissemination after fire is restricted due to the presence of the lichen mat; b) that most seed germination occurred on seedbed micro-sites created by higher fire severities; and c) that the presence and abundance of ant nests increased the amount of available seedbed for spruce, thereby influencing seedling establishment. In conjunction with the testing of seedbeds, the distribution of cone crop, amount and distribution of available seed in the burned area and along its perimeter were measured. By factoring in cone crop and seed rain with type and proportion of seedbeds, the study attempted to assess the pattern of, and factors that affect, black spruce recruitment in the lichen woodland community following fire.

1.3 STUDY AREA

1.3.1 Terra Nova National Park

TNNP is on Newfoundland's east coast (Figure 1), part of Canada's boreal forest and comprised of both the Central and North Shore Ecoregions (Damman, 1983). The park covers approximately 400 km^2, of which nearly 80% is forested. Forests are dominated by black spruce and balsam fir (*Abies balsamea* (L.) Mill.), with varying mixtures of white birch (*Betula papyrifera* Marsh.), mountain birch

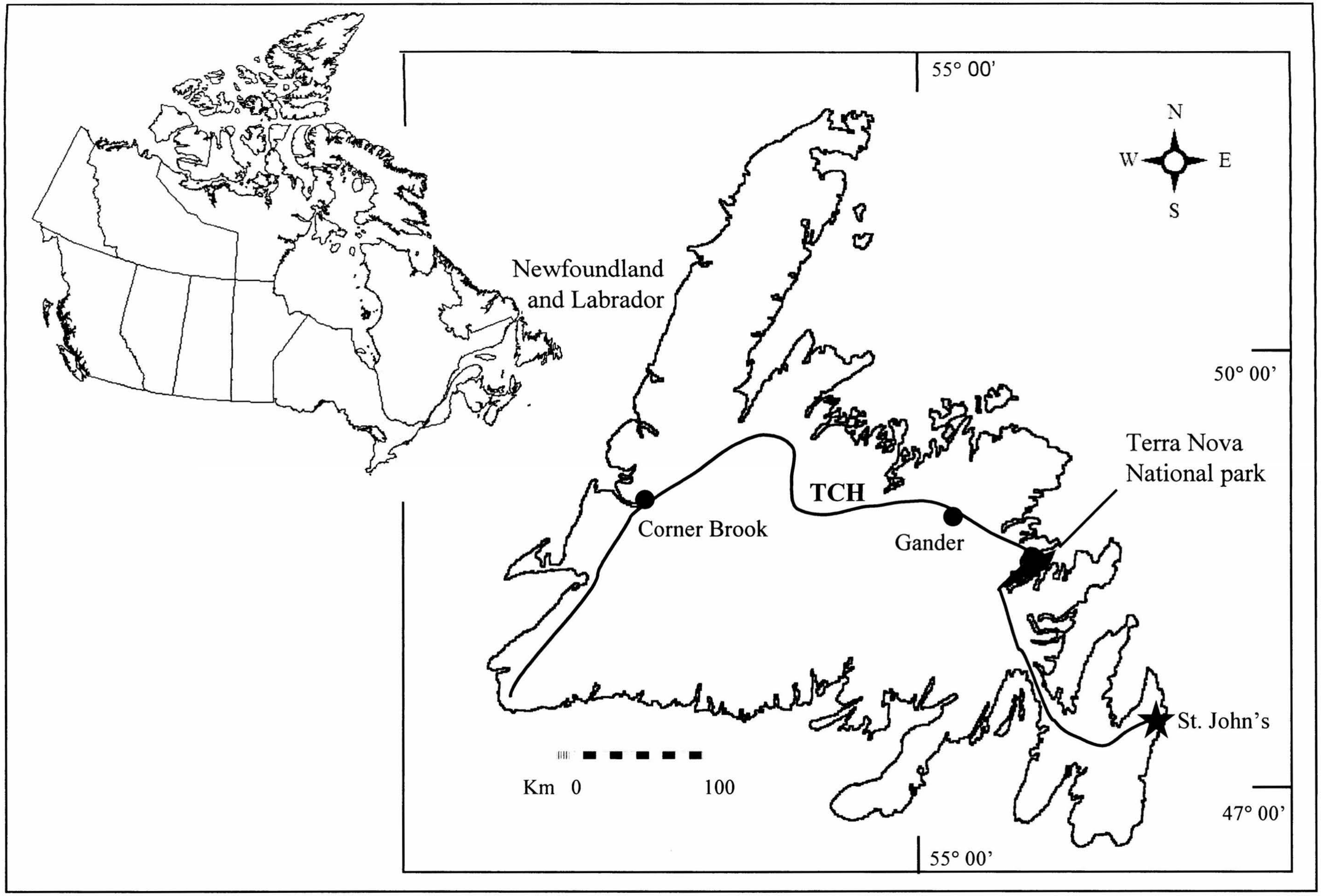

Figure 1. Map showing the location of Terra Nova National Park on the island of Newfoundland.

(Betula cordifolia Regel), trembling aspen (*Populus tremuloides* Michx.) and to a lesser degree, larch (*Larix laricina* (du Roi) Koch), white pine and red maple (*Acer rubrum* L.). Fire-adapted ericaceous shrubs including sheep laurel (*Kalmia angustifolia* L.), Labrador tea (*Rhododendron groenlandicum* (Oeder) K.A. Kron & W.S. Judd) and blueberries (*Vaccinium angustifolium* Aiton; *Vaccinium boreale* Hall & Aalders) are also common. Fireweed (*Epilobium angustifolium* L.), wild sarsaparilla (*Aralia nudicaulis* L.), and bracken fern (*Pteridium aquilinum* (L.) Kuhn) are common understory plants. Non-forested area is primarily composed of bogs and fens, with heath and rock barren scattered throughout.

Black spruce communities are the most common types in the park and include mainly black spruce-feather mosses on various soils, *Kalmia*-black spruce, *Sphagnum-Kalmia*-black spruce, *Cladina-Kalmia*-black spruce, and *Cladina*-black spruce (lichen woodland). Balsam fir is a major component on moist, well-drained soils and forms three community types based on soil-site conditions: *Hylocomium*-balsam fir, *Pleurozium*-balsam fir and *Rubus*-balsam fir. Deciduous communities are rare and most hardwoods are mixed with spruce or fir (Power, 2000).

TNNP is subject to overland prevailing westerly winds; therefore its climate is mostly continental. However, the area experiences a maritime influence due to its proximity to the Atlantic Ocean and extensive coastline. Climate is marked by brief, cool summers and moderate winters. Annual mean temperature is 4.4 °C and total annual precipitation averages 1184 mm, 75% of which falls as rain. Mean summer (May to September) temperature is 12.6 °C and total mean summer rainfall is 461 mm. Summer

winds are generally southwest and average 20 km per hour. Average relative humidity during summer is 66% (Environment Canada, MSC, 2001).

1.3.2 The Lichen Woodland Community

The lichen woodland in TNNP is located at Easting 723 250, Northing 5 379 850 (53° 58' 35" Longitude, 48° 31' 55" Latitude) and is 16 metres above mean sea level (Figure 2). The main tree species are black spruce and larch, although a few isolated white pine and white birch exist. Stand densities are low and black spruce are arranged primarily in clumps. Dominant trees in the community are in a 100+ year age class (Power, 2000). Ground vegetation is comprised of an ericaceous shrub layer (*Kalmia angustifolia, V. angustifolium, Rhododendron groenlandicum* and *Rhododendron canadense* L.) underlain by an extensive carpet of lichens (*Cladina stellaris* (Opiz) Brodo and to a much lesser extent, *Cladina rangiferina* L.) plus feather mosses (*Pleurozium* spp. and *Hylocomium* spp.). A sparse assemblage of herbs is also present. The soil underlying the area is nutrient-poor and is a podzolic, well- to rapidly-drained, sandy, gravel loam. Charcoal in the upper (Ae) soil horizon has shown that fire has led to the development of the lichen woodland in TNNP, and stand age reveals that it last occurred somewhere in the late 19th or early 20th century (Power, 1996).

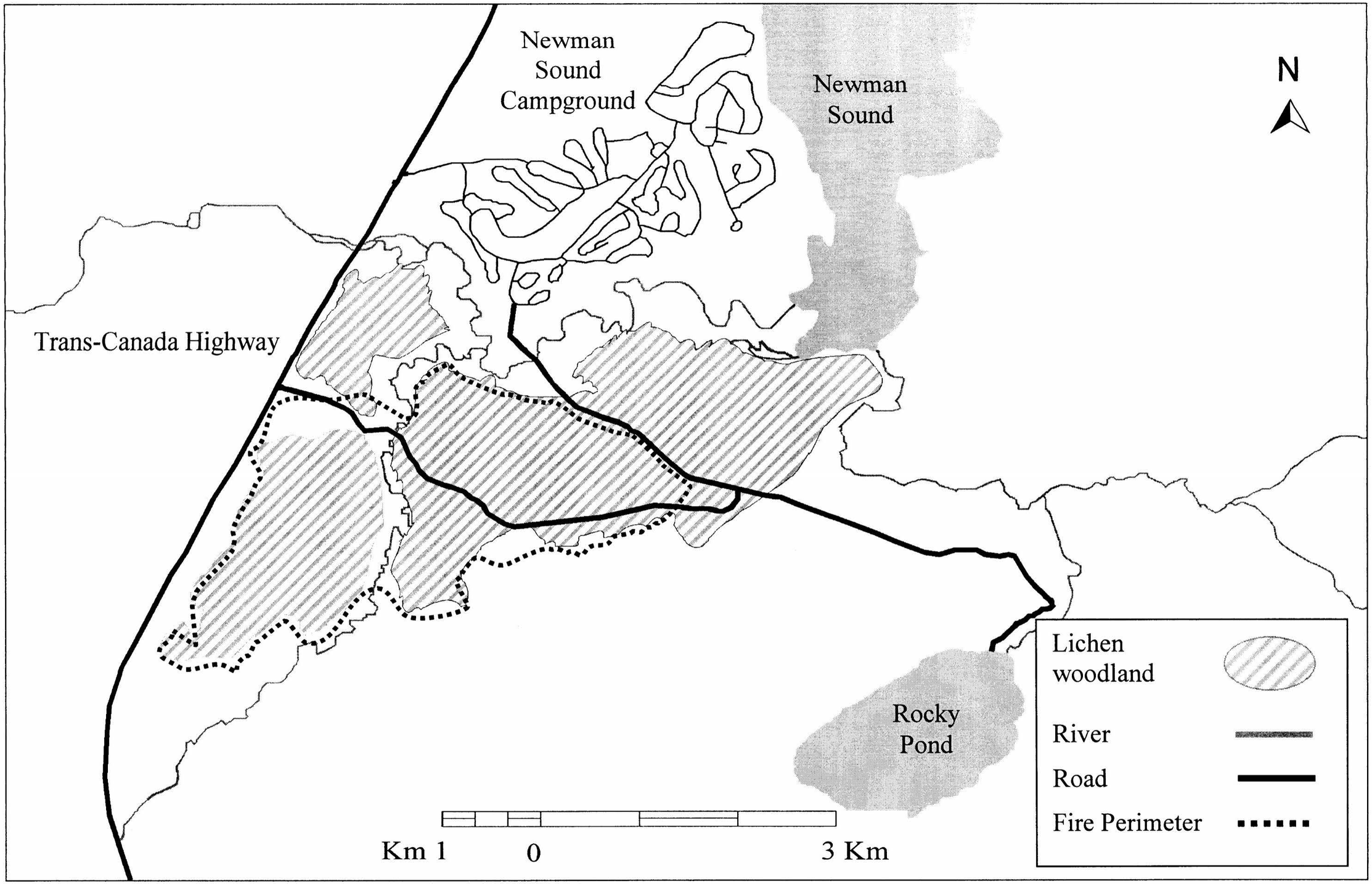

Figure 2. Map depicting the extent of the lichen woodland in TNNP.

1.4 FIRE BEHAVIOUR AT ROCKY POND

The fire at Rocky Pond involved two primary fire intensities. Intensity is expressed as a function of the weight of fuel consumed, the heat of combustion and the rate of spread of the fire (Byram, 1959). For the purposes of this study, since the rate of spread of the fire was estimated as a constant at 10 m per minute and the latent heat of combustion would be constant for the generally uniform vegetation throughout the entire area, the difference in fire intensity between the two areas was the difference in the amount of fuel consumed. The majority of the area was an area of high fire intensity in which many fine fuels including tree needles, small branches, twigs and a portion of the lichen layer were consumed by fire. A smaller area of lower intensity (10% of the burned area) - the head fire flanks and areas of back burning – resulted in an area where tree needles and small branches were not consumed by fire but were damaged by heat (Figure 3). Within lower intensity burned areas, some tree crowns were unburned but appeared to show signs of heat stress (e.g. yellowed needles). Within the affected area, burn severity (depth of burn) varied depending on whether it was an open area or under canopy. In areas occupied by the lower bulk density lichen mat, there was insufficient downward heat to burn away the full lichen or duff layer (Figure 4). In areas under dense black spruce canopy, where the fuel load was greater and produced greater heat, fire was more severe.

Figure 3. Lichen-woodland community after a fire that burned under two intensities (low on left, high on right).

Figure 4. Differences in the forest floor as a result of differences in fire severity. In the area on the left, remnants of the former lichen mat are visible and the duff layer below is relatively intact. In the blackened area to the right, burning of lower branches produced greater heat and therefore greater reduction in the duff layer.

CHAPTER 2: METHODS

2.1 STUDY AREA SAMPLING AND STRATIFICATION

The fire resulted in two separate burn intensities - high-intensity and low-intensity - experiments were set up in both of these distinct study areas. An unburned portion (30 ha) of the lichen woodland was used as a control. Experiments considered the four potential seedbeds available in both fire intensities: 1) high-severity burns beneath former tree canopies; 2) low-severity burns covered by partially consumed lichen mat and areas of exposed mineral soil due to the presence of 3) active ant nests or 4) abandoned ant nests (Table 1).

Table 1. Stratification of the study area by fire intensity and by seedbed.

High Intensity	Low Intensity
High Severity Burn	High Severity Burn
Low Severity Burn	Low Severity Burn
Active Ant Nest	Active Ant Nest
Abandoned Ant Nest	Abandoned Ant Nest

To facilitate sampling and to guarantee randomness and area coverage, a map was generated for the site using 80 data points placed 100 metres (m) apart in a grid (Figure 5). These points were generated on the Park's geographic information system (GIS) and converted to global positioning system (GPS) waypoints. Data from seedling surveys, cone collections, seed traps and duff cores were collected utilizing all or a subset of these 80 points.

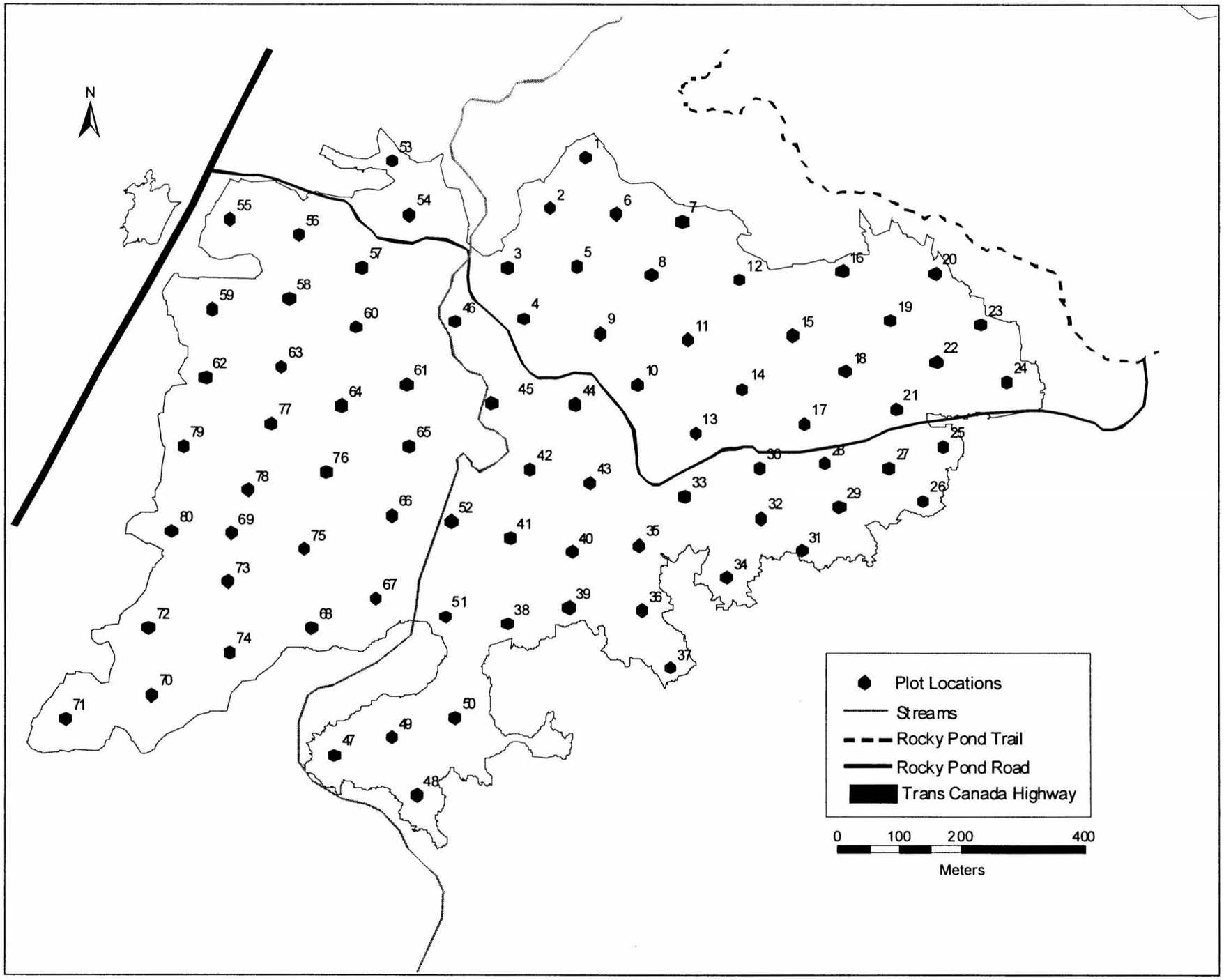

Figure 5. Map of burn area with 80 GPS data points plotted.

2.2 FIRE EFFECTS ON AVAILABLE SEEDBED

Ten 20x20 m plots were placed randomly throughout the burned area, five in high- and five in low-intensity burned areas. A twenty-meter distance was measured from a staked corner by running a metre tape along the western plot edge. Trees, tree clumps and ant nests were mapped by measuring the distance along this baseline tape and by taking a perpendicular measurement with a second metre tape from the baseline to each tree, clump or nest. Sketches were completed on a 20x20 grid, with each square on paper representing a square metre on the ground. The percent cover of high-and low-severity fire and ant nests was calculated using the information from the grid map.

Eight 1-m^2 ground plots were established within each 20x20-m plot to compare burn severity under tree canopy cover (4 plots) and in the open (4 plots) by measuring duff depths. There were no measurements of duff taken before the fire, so consumption was estimated by calculating the difference in duff depth between unburned and burned areas. In the unburned area, duff, lichen and feathermoss depth was measured to ± 1cm. Two survey pins were placed diagonally at the southwest and northeast corners of each 1-m^2 plot and measurements were taken at those points. In the burned area, duff and lichen depth measurements were taken in a similar manner.

Using the numbered sampling point map (Figure 5), all locations that were inside the lichen-spruce woodland - both burned and unburned - were visited in 2003. At each location a 100-m^2 circular plot was used to count and measure active and abandoned ant nests. Active nests were defined as raised, dry mounds where ant activity was observed. Inactive nests were flat, with more compact, moist soil and no ant activity. Nest length,

width, and status (active or abandoned) were recorded. Stratification for the nest survey was based on burned and unburned areas and not stratified by intensity, because the low-intensity burned area was too small and the number of grid points therefore too few for adequate comparison. Ants were collected randomly from nests throughout the lichen woodland and identified to species group (Larson, pers. comm. 2001).

2.3 FIRE EFFECTS ON CONE CROP AND SEED RAIN

A map of cone production was produced for the burned area. Cone crop data were collected at each of the 80 sampling points (5 were later excluded because they were in unburned areas or were outside of the lichen-woodland community). At each point the following data were collected: plot number, black spruce clump number, number of black spruce per clump, total number of black spruce and total number of black spruce bearing cones. The percent of black spruce with cones was calculated. Additionally, ten sites were sub-sampled and cones from the most recent crop year of each tree were collected to check for seed and to estimate the number of cones in the crowns.

To determine the level of red squirrel cone predation, black spruce cone counts were conducted along the burn perimeter where squirrel activity was highest. Twelve locations were chosen randomly and trees were selected for counting if they contained current year (2003) cones in the crown. Cones on four to six trees were counted at each location using a method similar to that employed by Tulk (2004), using binoculars for counting from an established and marked viewing point. Data were collected in late

August and the same sites were revisited in late November, after the main period of cone predation by squirrels (Tulk, 2004).

To estimate the amount, extent and distribution of seed fall in the burn area, two methods were employed – seed traps and duff core collection. Duff core collection gathered seed fallen before and immediately since the fire and seed traps continued seed collection into the subsequent year. From 31 July to 13 August 2003, duff collections were taken at 63 of the 80 locations within the burned lichen woodland community (17 were excluded because they were in unburned areas or were outside of the lichen-woodland community). At each location, four duff samples were collected with a sharpened 8-cm diameter galvanized pipe, 14 cm long with a welded handle and a foot pedal, which facilitated duff removal. Each sample constituted a 49-cm^2 area (0.005 of a square metre) thus 196 cm^2 of material was collected at each location. Duff samples were placed in labelled paper bags and air-dried at room temperature. Once samples were dry they were re-closed and stored in a dry area until examined. One of the four duff samples taken from each location was randomly chosen and examined for seed. Samples were spread over a light table and all seeds were removed, identified and counted.

Seed traps were constructed of 2.5x5 cm lumber to form a 61x61-cm frame with fibreglass fly screen attached to the bottom to catch seed and 2.54-cm^2 (1-$inch^2$) wire mesh on top to prevent seed removal by mammals and birds (Figure 6). Each trap constituted an area of 0.258 m^2. Seed traps were deployed 12 June 2002 in 20 of the 80 sample locations and were placed in pairs, across two areas of the lichen woodland. Every two weeks, seed traps were checked and seed removed. Number of seeds per trap

was determined and seed density per hectare was calculated. A map of the burned area showing distribution of seed rain by species was created.

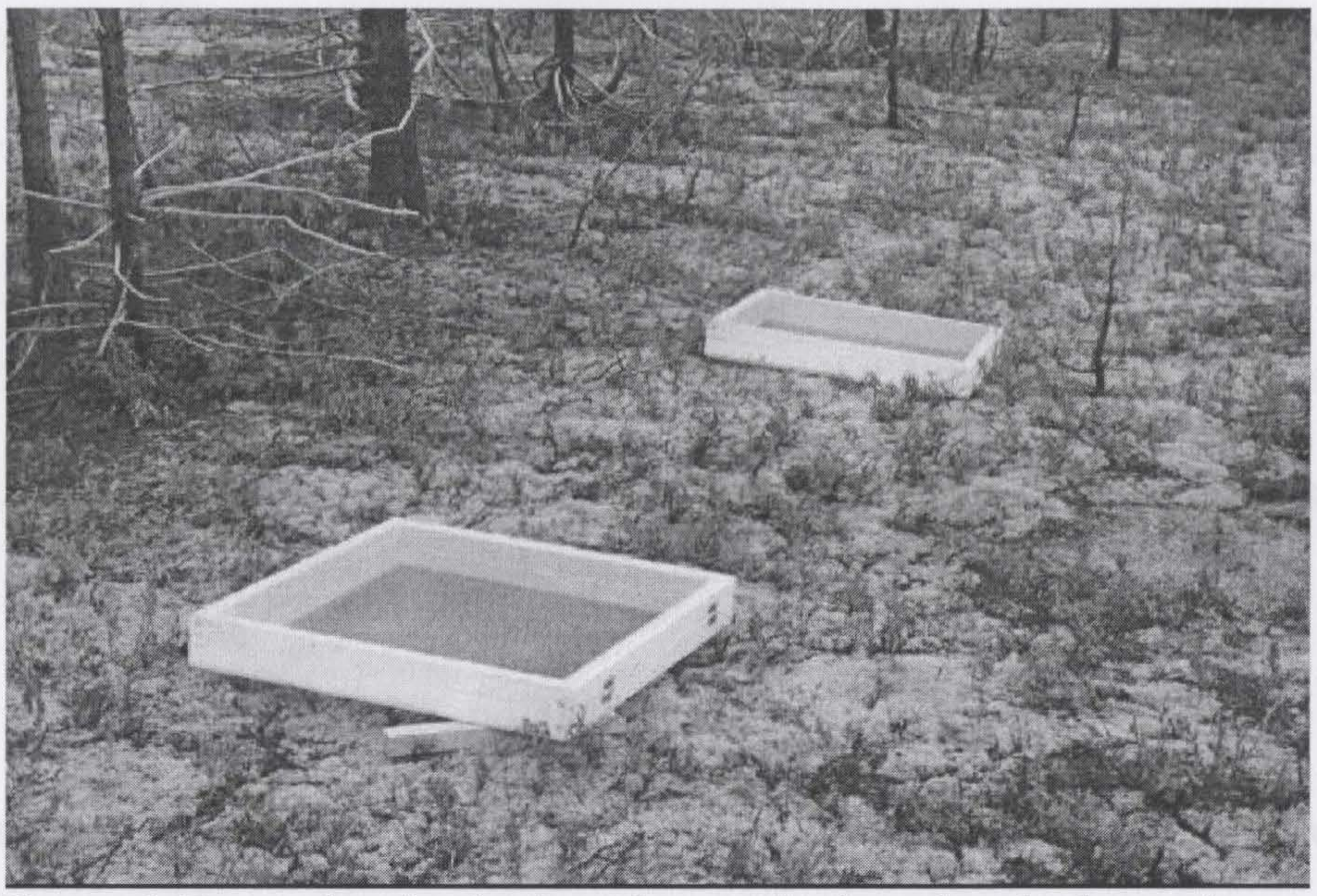

Figure 6. Example of paired seed traps deployed at the burn site.

2.4 SEEDBEDS AND BLACK SPRUCE GERMINATION

For the two classes of fire intensity a seeding experiment was carried out to test if burning provided the necessary seedbed required for tree establishment. Ten sites were selected throughout the burned area: five in the high- and five in low-intensity burned area, each separated by at least 40 m. At each site five 30x30-cm plots were established on four different seedbeds along with a control. Seedbeds were: 1) low severity (lichen mat/duff substrate); 2) high severity seedbed (scorched duff at the base of a former tree clump); 3) active ant nest and 4) abandoned ant nest. Control plots consisted of a commercially available, standard potting soil in shallow planting trays and were used as

an indication of the extent that micro-climatic factors, rather than seedbed, played in germination success. A 10x10-cm grid was placed over each plot and these plus the controls, were seeded with 100 black spruce seeds on 20 June, 2003. Seeds used in the study originated from black spruce in the TNNP area and were stored at the provincial tree nursery at Wooddale, Newfoundland and Labrador. Seeds obtained from the nursery had been tested and assigned a viability of > 90% (B. Linehan, pers. comm. 2003)

Each study area was visited weekly throughout the growing season (June until two consecutive weeks in late fall with no new germination, or after heavy frost) and seedlings were searched for and identified using coloured toothpicks. The fate of all seedlings was monitored until the end of the experiment or until mortality due to predation or drought. In the spring of 2004, seedlings that had survived to the end of the 2003 growing season were inspected for over-winter survival.

A seedling survey was also conducted to record the number of naturally occurring seedlings in relation to the four seedbeds. During the week of 11-17 September, after naturally germinated seedlings would have grown enough to be visible, a survey was carried out at all 80 sampling points, except for numbers 23, 48, 53, and 54, which were not in the lichen woodland, and number 78, which was not burned. At each location, four random 1-m^2 plots were chosen and surveyed, one plot for each of the same four seedbeds in the seeding trials. For all seedlings surveyed, the seedbed was recorded, the seedling was tagged and a GPS location recorded. All other seedlings coincidently observed outside of the surveyed plots were additionally (and separately) noted and their seedbeds identified.

2.5 CLIMATE AND MICROCLIMATE

As drought is known to limit recruitment (Moss, 2004), to characterize soil moisture conditions that could influence seedling germination and survival, two sites representing high-intensity and low-intensity burn lichen woodland forest were selected to sample soil moisture. At each site, a soil moisture monitoring tube was placed in the low severity duff/lichen mat, an abandoned ant nest, an active ant nest and a high severity burned clump and beginning 27 June (the start of the seeding trial), soil moisture as a percentage (m^3/m^3) was collected weekly from each site at each location using a Delta-T PR1 Profile Probe®. Readings were gathered at depths of 10, 20, 30 and 40 cm from the soil surface. Three readings were taken at each depth, by rotating the probe 120 degrees after each reading. The three readings were averaged for each depth. Soil moisture was taken every seven days unless it rained (as the moisture probe will give less accurate readings during rainfall). In those instances readings were taken the next available dry day. Since new seedlings would take root in the upper 10 cm of the soil, only readings taken at the 10-cm depth were analysed in this study. To estimate the on-site temperature and relative humidity that would influence seedling germination and survival, Hobo Pro® temperature and relative humidity data loggers were also placed in two sites representing high-intensity and low-intensity burn. Temperature (^{O}Celsius) and relative humidity (percent) were recorded at one-hour intervals. Weather data such as daily mean and maximum temperatures and precipitation were obtained from the Park weather station located nearby.

2.6 DATA ANALYSES

The seeding trial was set up for the purpose of using the general linear model (Nelder and Wedderburn, 1972) and a repeated measures MANOVA design. Two factors (seedbed and burn intensity) were analysed within a randomized block design and data in the experiment were treated as repeated measures, with 15 replicate sampling dates. Analysis was performed on the number of seedlings present on each sampling date. Additional analysis involved comparison of survival distributions for the seedbeds. Survival curves and estimates of survival time using mean seedling survival time in weeks were generated using the Kaplan-Meier method and analysed using the Mantel-Haenszel log-rank test (Motulsky, 1995). Control plots were established as an indication of the role that climatic factors, rather than seedbed, played in germination success, so they were excluded from statistical analysis. Analysis of variance (ANOVA) and paired t-tests were used to compare differences in duff depth between unburned and burned area, between high- and low-intensity burned areas and between high- and low-severity burned areas. ANOVA was also used to assess differences in soil moisture at 10-cm depth for the four seedbeds. Paired t-tests were also used to compare differences in number of ant nests and ant nest size between burned and unburned areas. Alpha was set at 0.05 significance for all statistical tests and (for individual paired t-tests), was corrected for multiple tests using the Bonferroni adjustment ($\acute{\alpha} = 0.05/6$ tests $= 0.0083$) (Sokal and Rohlf, 1995). For all F-tests, residuals were checked for independence, normality and homoscedasticity.

CHAPTER 3: RESULTS

3.1 FIRE EFFECT ON AVAILABLE SEEDBED

3.1.1 Fire Effects on Duff and Lichen Depth

The June 2002 wildfire did not burn to the mineral soil, but duff depths were reduced. In open areas (between spruce clumps), depths between burned and unburned areas differed by 2.61 cm ($t_{[78]} = 8.49$; $p < 0.0001$), an average indicating a reduction in duff depth of 48% (Table 2). Under tree canopy the difference was 4.24 cm, a reduction of 41% ($t_{[78]} = 5.59$; $p < 0.0001$). The amount of duff burned by fire under tree canopies was greater, but the proportion consumed was similar to that in the open.

Table 2. Descriptive statistics for measured depth (cm) of organic soil (duff) between the burned and unburned areas and between burn intensities for both the open and canopy conditions.

	Open		Canopy	
	Mean ± SD (N) (cm)	Range (cm)	Mean ± SD (N) (cm)	Range (cm)
Unburned	5.45 ± 2.29 (40)	0.0 - 12.0	10.38 ± 5.71 (40)	0.0 – 21.0
Burned	2.84 ± 1.08 (80)	0.0 - 5.0	6.14 ± 2.61 (80)	1.0 - 15.0
Low Intensity	2.94 ± 0.93 (40)	1.0 – 5.0	6.88 ± 2.72 (40)	1.0 - 15.0
High Intensity	2.74 ± 1.22 (40)	0.0 – 5.0	5.40 ± 2.29 (40)	1.0 - 11.0

Significant differences in duff depths between unburned and high and low intensity burned areas, were due to effects of canopy cover ($F_{[1, 234]} = 100.41$, $p < 0.0001$) and burn intensity ($F_{[2, 234]} = 37.10$, $p < 0.0001$). Differences in duff depth between high and low intensity burns under canopy was 1.48 cm and significant at $\alpha = 0.05$ but not at ά

= 0.0083 ($t_{[78]} = 2.25$, $p < 0.02$). The mean difference in duff depth between high and low intensity in the open was only 0.21 cm and was not significant ($t_{[78]} = 0.78$, $p < 0.2$). In the open condition, the duff in the low intensity burn was reduced by 46% relative to the unburned duff and in the high intensity burn, reduced by 50%. Under canopy, comparable reductions were 33% and 48% respectively. In summary, more duff was consumed under tree canopies, and duff was shallower in the high intensity burn.

The lichen layer was greatly impacted by the fire. It was reduced in thickness by as much as 88% (Table 3), with a significant difference ($F_{[2, 137]} = 346.95$, $p < 0.0001$) between the unburned and burned areas. Regardless of intensity, reduction of the lichen layer was similar throughout the burn, as differences in post-burn lichen depth between the two intensities were not statistically significant ($F_{[1, 78]} = 1.36$, $p = 0.25$).

Table 3. Descriptive statistics for measured depth (cm) of the lichen layer between the unburned and high and low intensity burned areas.

	Mean ± SD (N)	Range
Unburned	12.52 ± 3.28 (60)	0.0 - 19.0
Low Intensity	1.49 ± 1.20 (40)	0.0 – 4.0
High Intensity	1.86 ± 1.64 (40)	0.0 – 6.0

The effects of higher fire severity around the base of black spruce resulted in a difference in the amount and type of post-fire seedbed. Black spruce were arranged primarily in clumps (Figure 7) with a mean clump density of 445.3 ± 270.5 per ha and a mean of 9.2 ± 6.3 stems per clump. In terms of potential seedbed area, the mean area covered by scorched black spruce clumps was 2132.5 m^2 ± 954.0 m^2 per ha – an

estimated average total of 20.9 ha (2132.5 x 98 ha). Thus, 21.3% (20.9 ha/98 ha) of the burned area consisted of seedbed generated by high-severity fire.

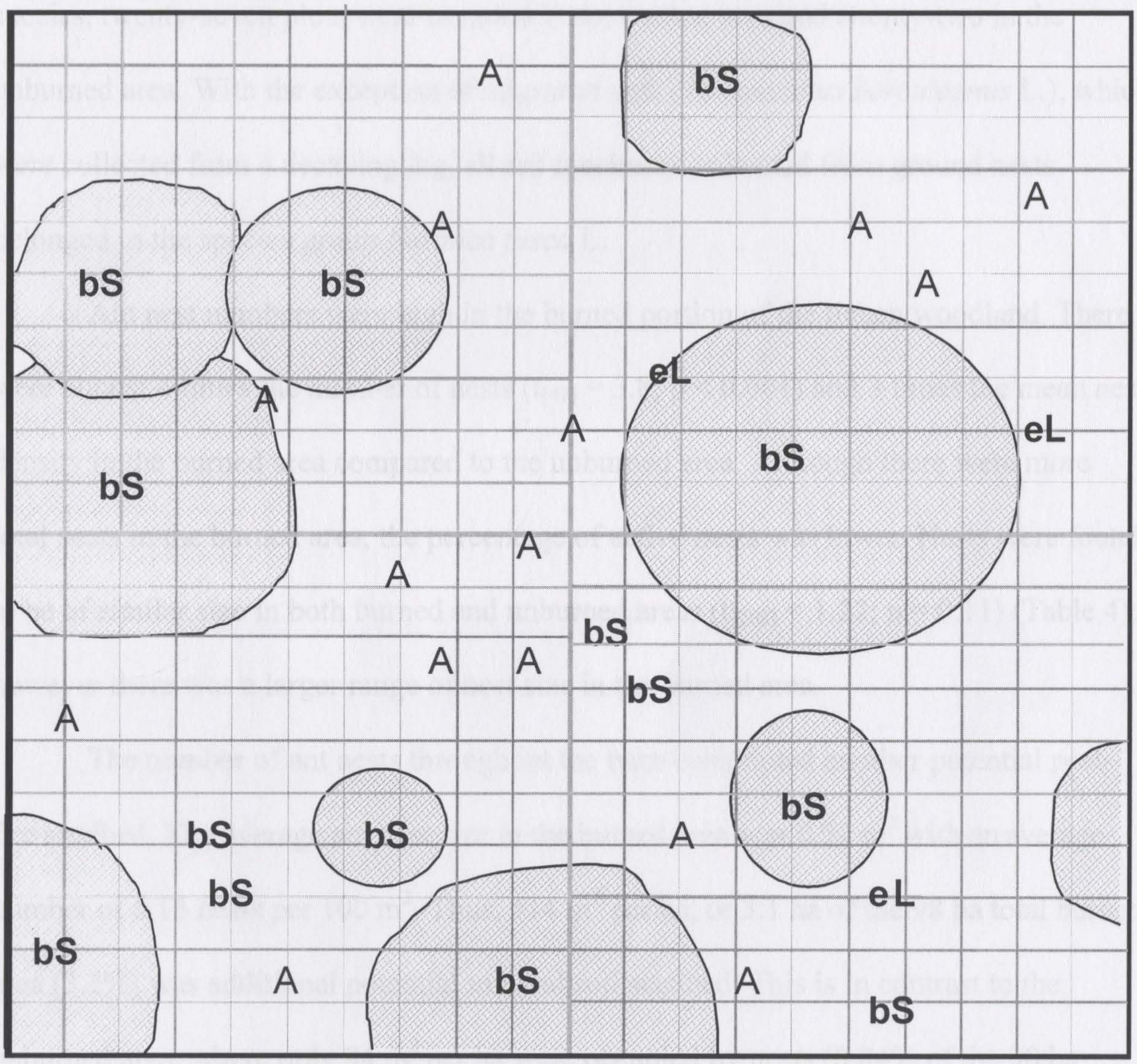

Figure 7. A representative 20x20 m tree map depicting the spatial arrangement of individual trees, black spruce clumps and ant nests. bS - black spruce, eL - eastern larch, A - ant nest. Only single and clump centre bS are depicted; extent of clumps with lichen-free scorched duff beneath are shown (shaded areas).

3.1.2 Fire Effects on Number and Size of Ant Nests

In order to count and measure active and abandoned ant nests and to identify species, twenty-seven plots were sampled in the burned area and twenty-two in the unburned area. With the exception of carpenter ants (*Camponotus herculeanus* L.), which were collected from a decaying log, all ant specimens collected from ground nests belonged to the species group *Formica fusca* L.

Ant nest numbers were high in the burned portion of the lichen woodland. There were almost 4 times the number of nests ($t_{[47]} = 3.8$; $p < 0.001$) and 3 times the mean nest density in the burned area compared to the unburned area. Although there were more total nests in the burned area, the percentage of active nests was lower. Nests were found to be of similar size in both burned and unburned areas ($t_{[208]} = 1.22$; $p = 0.11$) (Table 4), however there was a larger range of nest size in the burned area.

The number of ant nests throughout the burn constituted another potential post-fire seedbed. The average ant nest size in the burned area was 0.51 m^2 with an average number of 6.15 nests per 100 m^2. Thus, 314 m^2 per ha, or 3.1 ha of the 98 ha total burned area (3.2%) was additional potential mineral soil seedbed. This is in contrast to the unburned area, where only 84 m^2 per ha were occupied by nests (0.84% of the 30 ha unburned area).

Table 4. Attributes of ant nests sampled for 100 m^2 circular plots including active and non-active nests.

Variable	Burned	Unburned
No. Nests	166	44
Density (No./100m^2)	6.15	2.00
Density Range (No./100m^2)	0 – 10.0	0 – 14.0
Mean nest size (m^2)	0.51 ± 0.48	0.42 ± 0.23
Size Range (m^2)	0.03 - 2.90	0.10 - 1.20
Percent Active	49	55

3.2 FIRE EFFECTS ON CONE CROP AND SEED RAIN

Pre-burn cone crop throughout the lichen woodland was low overall. Within the burn area, a total of 3266 black spruce were counted, of which only 8.9% (292) contained cones in the crown. The mean number of spruce with cones per 100-m^2 plot was 3.89 ± 3.27. Cone-bearing trees comprised less than half of all black spruce trees counted per plot although there were cone-bearing trees distributed throughout the burn area (Figure 8). Only six of the 75 plots sampled (9.3%) contained greater than 25% cone-bearing trees while ten (13.3%) had no cone bearing trees at all. Burn intensity did not effect the percentage of trees with cones remaining in the crowns, as there was no significant difference between percentage of trees with cones for high or low intensity ($F_{[1, 73]}$ = 0.128, p = 0.72). Likewise, the percentage of trees with cones located at the burn edge showed no difference compared with those located in the burn interior ($F_{[1, 73]}$ = 1.79, p = 0.18). Thirty cone-bearing trees had a mean of 23.8 ± 27.3 cones per tree (N= 715; median = 13.5). The number of cones per tree ranged from 1 to a maximum of 106. Although actual yield per cone was not evaluated, most burned cones contained little to no seed. Thus, a low number or cone-bearing trees combined with a low number of cones per tree translated to a low potential seed yield.

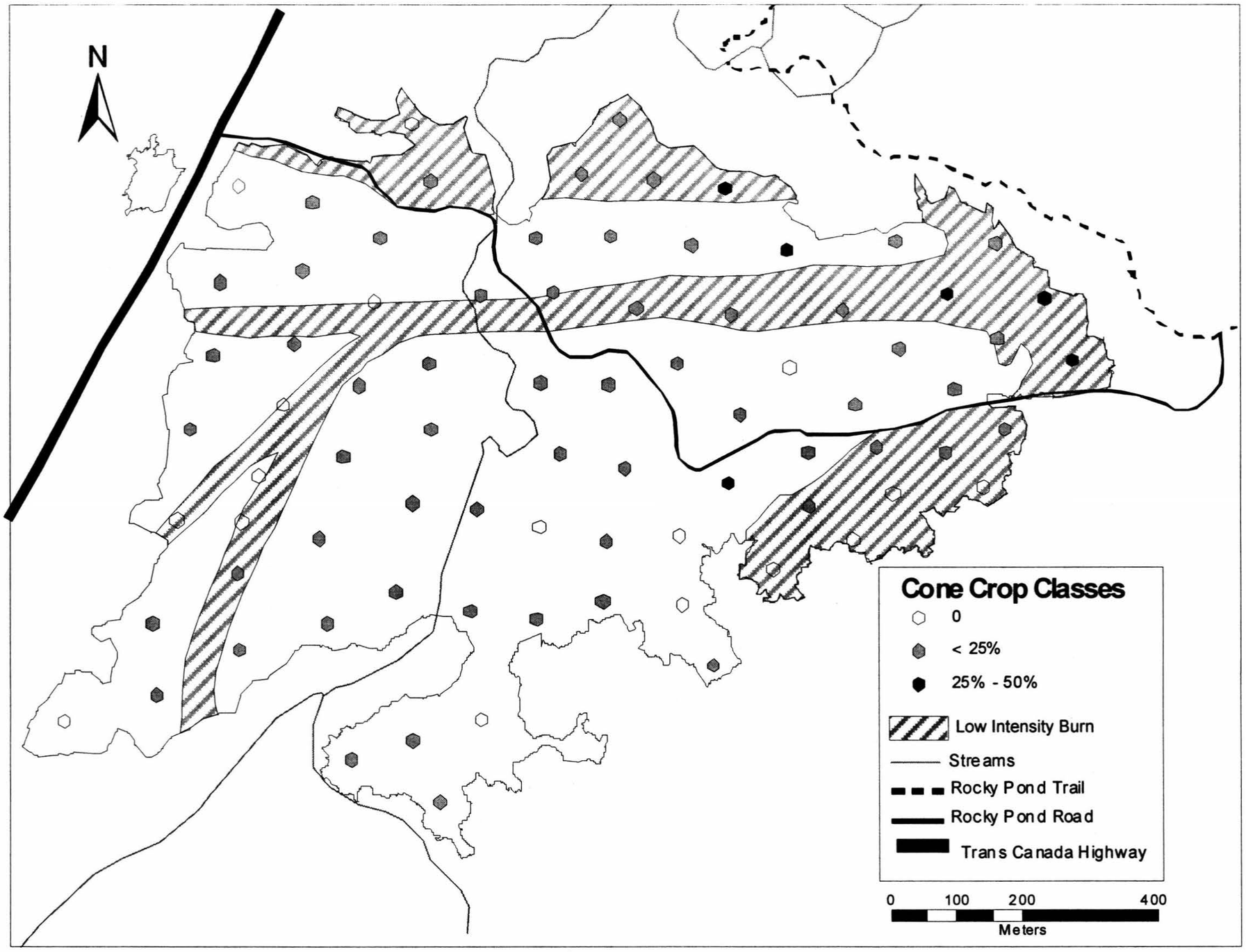

Figure 8. Map of cone production within the burn perimeter. Cone crop classes represent the percentage of cone-bearing trees sampled at each point.

Predation by red squirrels lowered seed yield further. No evidence of squirrel activity was witnessed throughout the burned area, but seed crop from the unburned edge was affected by predation. Along the burn perimeter, a total of 56 unburned, cone-bearing trees were counted in August. The mean number of cones per tree was 37.32 ± 42.80 (N = 2090; range = 3 to 224; median = 19). In November, after red squirrel predation, the mean was 17.82 ± 24.27 (N = 998; range = 0-123; median = 8). The percent of cones predated ranged from 0 - 100%, with a mean cone removal of 51.67% ± 33.65 (median = 51.56%). Thus, the already low seed source was reduced by nearly half.

Ninety per cent of seed traps captured seeds. For surviving black spruce seed, seed trap data showed that seed rain was light but fairly constant throughout the summer of 2003 (Figure 9). Black spruce seeds were captured in just over half (11 locations, or 55%) of seed trap locations and white birch in 75% (15 locations) and while 50% captured both white birch and black spruce (Table 5). Only 4 of the 40 seed traps at the 20 locations failed to capture any seed. Eastern larch seed was found in only one trap and was not captured until October. Most white birch was captured in the western portion of the burn, reflecting the presence of a small birch stand west and adjacent to the burn. Each trap constituted a 0.26 m^2 area with 0.43 black spruce seeds per trap, the equivalent of 1.65 seeds per m^2. Using trap data from 26 June to 27 November, an estimate of 16 539 black spruce seed per ha fell. In addition, 522 157 white birch seed and 1938 larch seed per ha had also fallen.

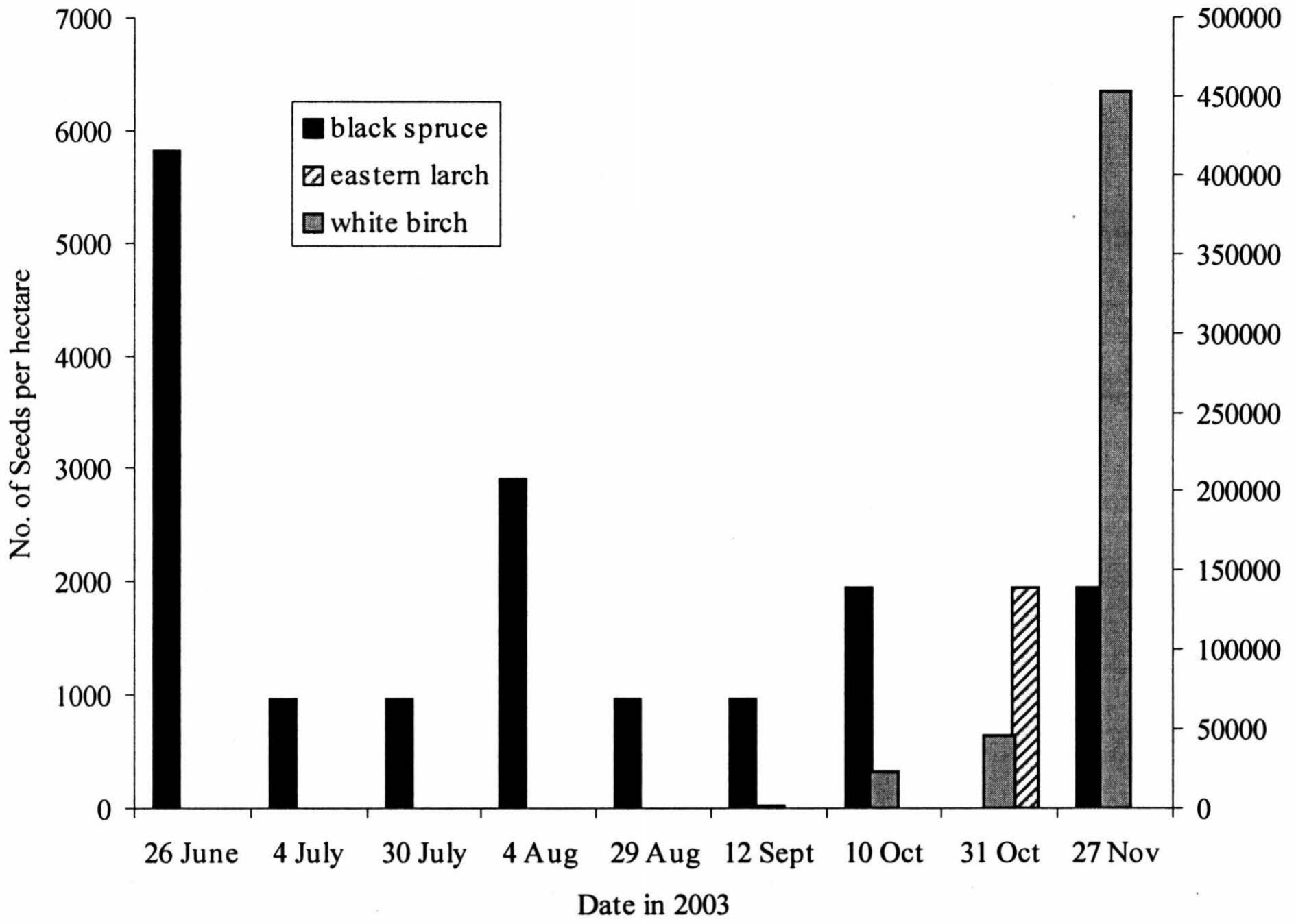

Figure 9. Average number of black spruce, eastern larch and white birch seeds per ha collected in seed traps in 2003, by collection date. The left Y- axis denotes black spruce and eastern larch while the right Y- axis denotes white birch.

Duff cores also indicated a relatively wide distribution of seed rain (Table 6). Nineteen of the 63 samples (30.2%) contained black spruce seed. A total of 46 black spruce seeds were counted from all duff samples analysed (46/63 = 0.73 seeds per sample). Since each core sampled constituted a 49.02 cm^2 area or 1/200th of a square meter, then 0.73 seeds per sample (X 200) was the equivalent of 146 black spruce seeds per m^2, or an estimated average of 1 460 000 seeds per ha. Only 2 cores contained white birch seed, the estimated equivalent of 64 000 seeds per ha. No core contained larch seed. Combining all seed rain data from duff sampling and seed traps, the equivalent of 1 476

539 black spruce seeds, 586 157 white birch seeds and 1938 eastern larch seeds per ha fell in the burned area.

Table 5. Estimated seed per hectare captured in seed traps located throughout the burn in 2003. Seed trap location numbers refer to the point sampling grid depicted in Figure 5.

Seed Trap Location	Total black spruce Seed	Total white birch Seed	Total eastern larch Seed
1	0	0	0
6	0	0	0
8	0	0	0
11	19 375	19 375	0
13	0	0	0
14	19 375	19 375	0
15	0	19 375	0
16	19 375	77 500	0
28	58 125	193 750	0
38	58 125	0	0
40	19 375	19 375	0
43	0	77 500	0
61	19 375	348 751	0
64	0	658 751	0
67	19 375	232 500	38 750
69	38 750	1 065 627	0
72	19 375	678126	0
75	38 750	775 002	0
76	0	542 501	0
79	0	5 715 636	0

Table 6. Number of seeds found in organic soil samples taken within the burn perimeter. Seed trap location numbers refer to the point sampling grid depicted in Figure 5.

Location	Total black spruce seed	Total white birch seed
7	1	0
11	1	0
12	1	0
13	1	0
19	3	0
20	1	0
22	2	0
25	0	1
30	1	0
39	3	0
42	3	0
43	1	0
44	1	0
49	5	0
55	2	0
56	12	0
60	1	1
63	1	0
64	1	0
65	3	0
70	1	0
76	1	0

3.3 SEEDBEDS AND BLACK SPRUCE EMERGENCE

3.3.1 Seeding Trials

Of the 5000 experimental seeds sown, only 69 of an estimated 4500 (90% of total sown) viable seeds germinated (1.5%). Seedlings began germinating in the fourth week after sowing (week ending July 18th) and continued germinating late into the fall (week ending October 31st) (Figure 10). The majority of seedlings did not emerge in the control plots until September when rain became more frequent, an indication of moisture deficit. Eleven seedlings germinated in the lichen mat, none in the active ant nests, nine in the abandoned ant nests, seven in the scorched duff and 42 in the control mix (Table 7). Of these 69 seedlings, 18 died during the first growing season – a survival rate of 74%. Only 27 seedlings germinated in natural seedbeds (excluding the control plots). Removing control seedlings from the calculation, the survival rate was 67%. The majority of seedling deaths in the natural seedbeds occurred in August.

Table 7. The total number of experimental seedlings that germinated and survived for each seedbed, through 2003 and after the winter of 2003-04.

Number of Seedlings	High Intensity	Low intensity	Total
Total Treatment	21	6	27
Lichen mat	10	1	11
Active ant nest	0	0	0
Abandoned ant nest	9	0	9
Scorched clumps	2	5	8
Control plots	2	40	42
Treatment seedlings survived (2003)	15	3	18
Treatment seedlings survived (2004)	8	2	10

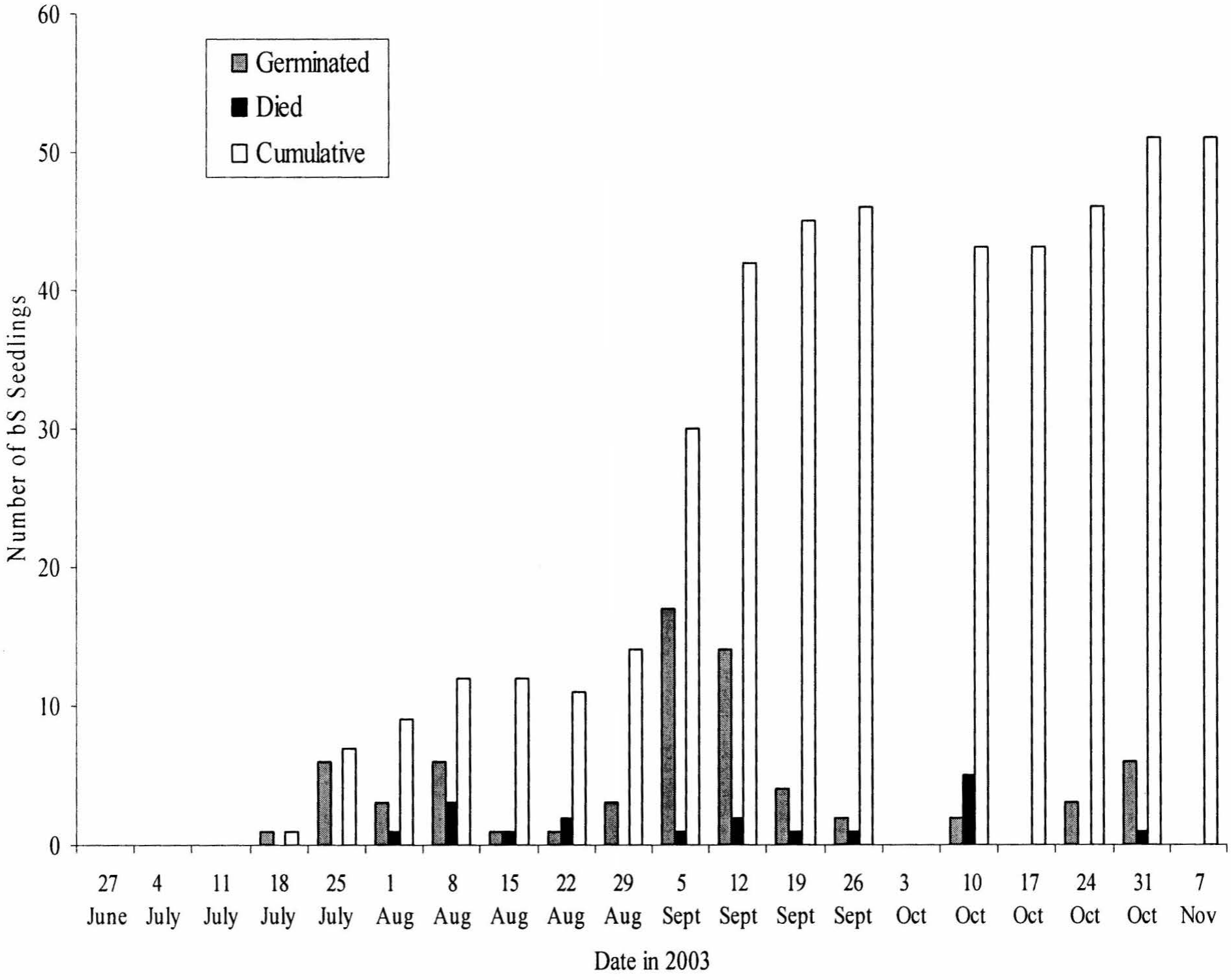

Figure 10. Total number of seedlings germinating each week, the number of seedlings that died and the cumulative number of seedlings week by week throughout the 2003 growing season (Note: No data collected on October 3).

Neither the block effect nor the interaction between seedbed and fire intensity were significant (Table 8). Due to the low number of seedling emergence and the high variability in responses for each seedbed, there were also no significant differences between fire intensities or among the four seedbeds. Differences were revealed by plotting the cumulative germination and cumulative survival for the seedbeds that produced seedlings (Figure 11). Year-end (27 November) survival was 64% for seedlings

in the lichen mat, 89% for abandoned nests, 52% for the control seedlings and only 29% for scorched duff. Cumulative germination and cumulative survival for the two fire intensities were similar – 57% for the high-intensity burn and 54% for low-intensity. The total number of seedlings in the low-intensity burn was higher due to the high number germinating in a single control plot (38 seedlings). Survival curves were generated for the three seedbeds (Figure 12) estimating mean survival times of 14.6 weeks for seedlings in the lichen mat, 15.4 weeks for seedlings in the abandoned ant nests and 9.3 weeks for those in scorched duff. Probability of survival differed significantly among the three seedbeds ($\chi^2_{[2,27]} = 6.652$; $p = 0.036$), due to the low survival rate of seedlings germinating in scorched duff.

Table 8. MANOVA summary table for 15 repeated measures of the number of living black spruce seedlings during the 2003 growing season.

Source	DF	SS	MS	F	P
Seedbed	3	33.8	11.3	0.71	0.556
Fire Intensity	1	26.5	26.5	1.66	0.208
Seedbed x Intensity	3	46.4	15.5	0.97	0.420
Block	4	25.2	6.3	0.40	0.810
Error	28	446.1	15.9		
Total	39	578.0			

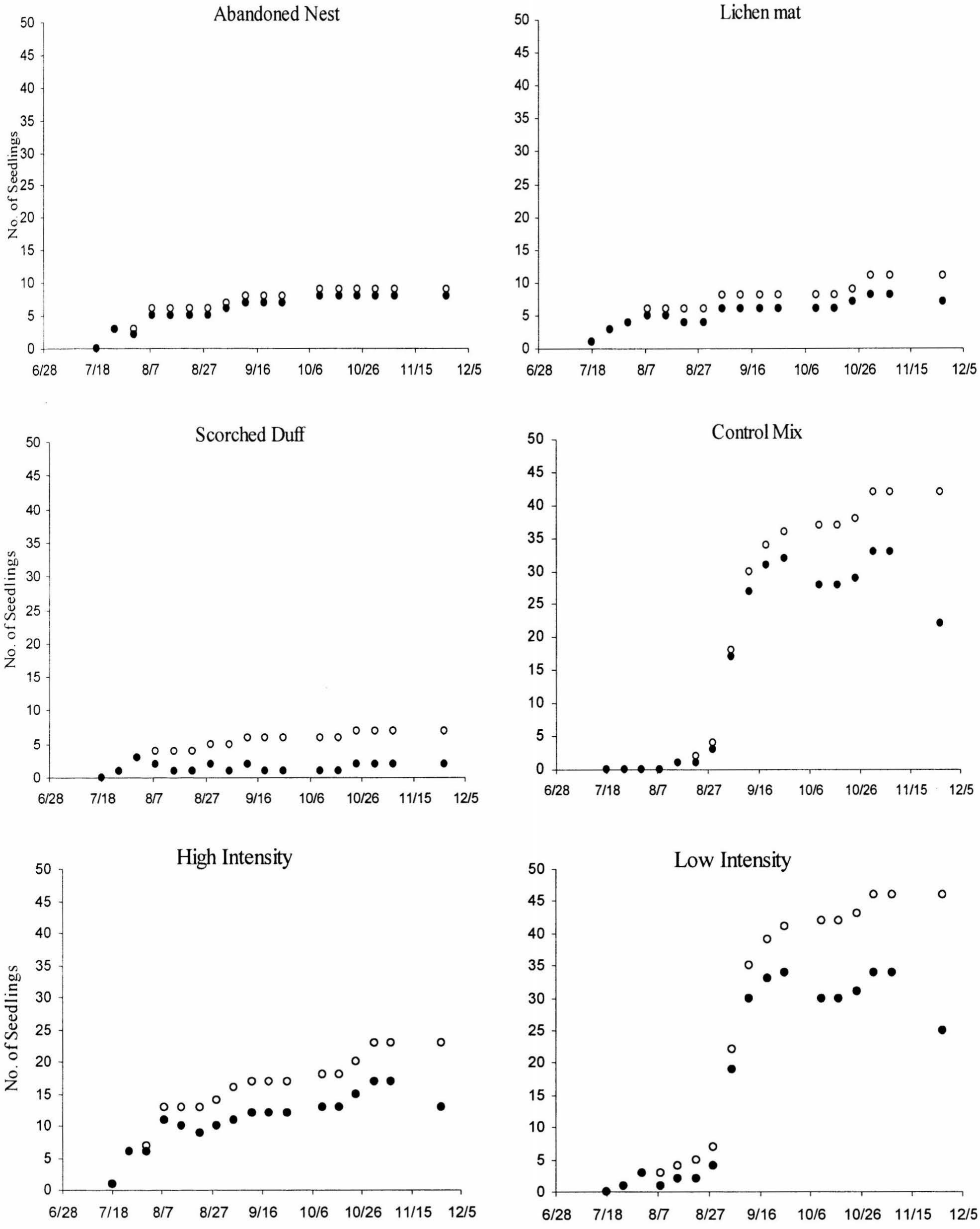

Figure 11. Cumulative germination (open circles) and survival (solid circles) of experimental black spruce seedlings for the four seedbeds and for fire intensity in the 2003-growing season (18 sampling dates).

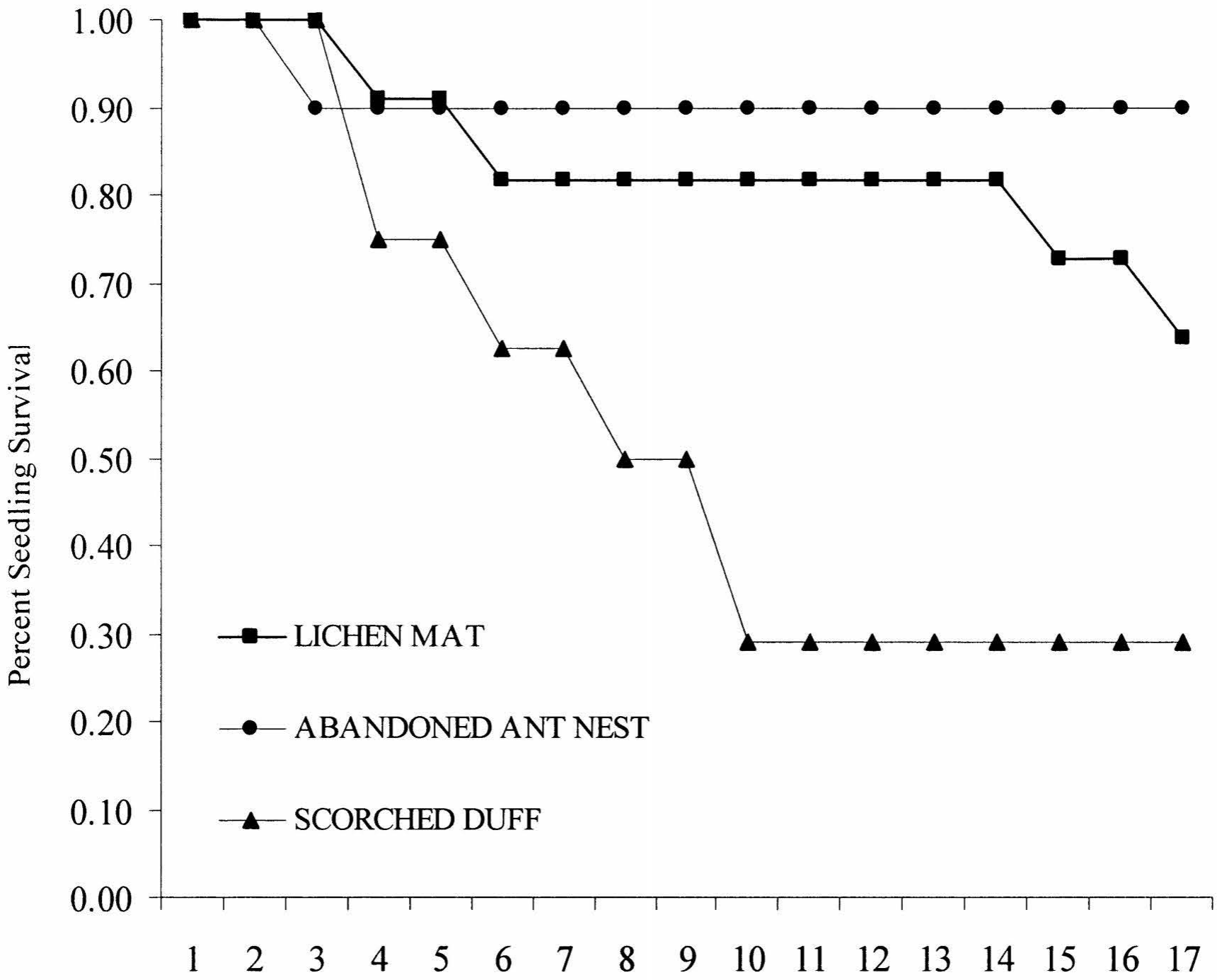

Figure 12. Survival probability of black spruce seedlings between seedbeds (Note: No seedlings germinated in active ant nests).

Over-winter (November 2003 to May 2004, inclusive) seedling survival was poor. In the high-intensity burned area, 4 out of 5 seedlings survived in the lichen layer, 4 out of 8 seedlings survived in the abandoned ant nests and both remaining control seedlings died. In the low-intensity area, the lone seedling survived in the lichen mat, 1 out of the 2 seedlings survived in the scorched duff and 19 out of 31 control seedlings survived. Overall, winter reduced the survival of seedlings to only 45% in the lichen mat, to 44% in the abandoned ant nests and to 14% in scorched duff. By May 2004, the survival rate of

seedlings in the high intensity burn declined from 57% to 35% while the survival in the low intensity burn remained similar (from 54% to 50%).

3.3.2 Seedling Survey and Comparison of Seedbeds

A total of 62 sites were surveyed and 13 naturally germinated black spruce seedlings were found: two in the lichen mat (15.4%), one at the edge of an active ant nest, (7.7%), five in abandoned ant nests (38.5%) and five in scorched duff beneath former spruce canopy (38.5%). The density of natural black spruce seedlings throughout the burned area was thus calculated as 524 seedlings per ha ($13/(4x1\text{-}m^2$ plots x 62) = 0.0524 seedlings per m^2). All naturally occurring seedlings found during the survey had germinated in the 2003 growing season. Scanning the area randomly resulted in an additional 24 seedlings being found: four in the lichen mat, one in an active ant nest, seven in abandoned ant nests, six in scorched duff beneath former spruce canopy and six others in other substrates such as along roadside and in soil from overturned trees. Four of these seedlings (16.7%) had germinated in 2002 and the rest in 2003. The patchy distribution of all seedlings is depicted in Figure 13. There appears to be no relation between percent available seedbed and percent germinants found on each (Table 9). However, in both cases the lowest germination occurred on active ant nests.

Table 9. Percent of available seedbed and percent of black spruce germinating on the four available seedbeds for the seeding trial and seedling survey.

	Lichen mat	Active nest	Inactive nest	Scorched duff
Percent available seedbed	75.9	1.6	1.6	20.9
Percent black spruce (trial)	40.7	0.0	33.3	25.9
Percent black spruce (survey)	15.4	7.7	38.5	38.5

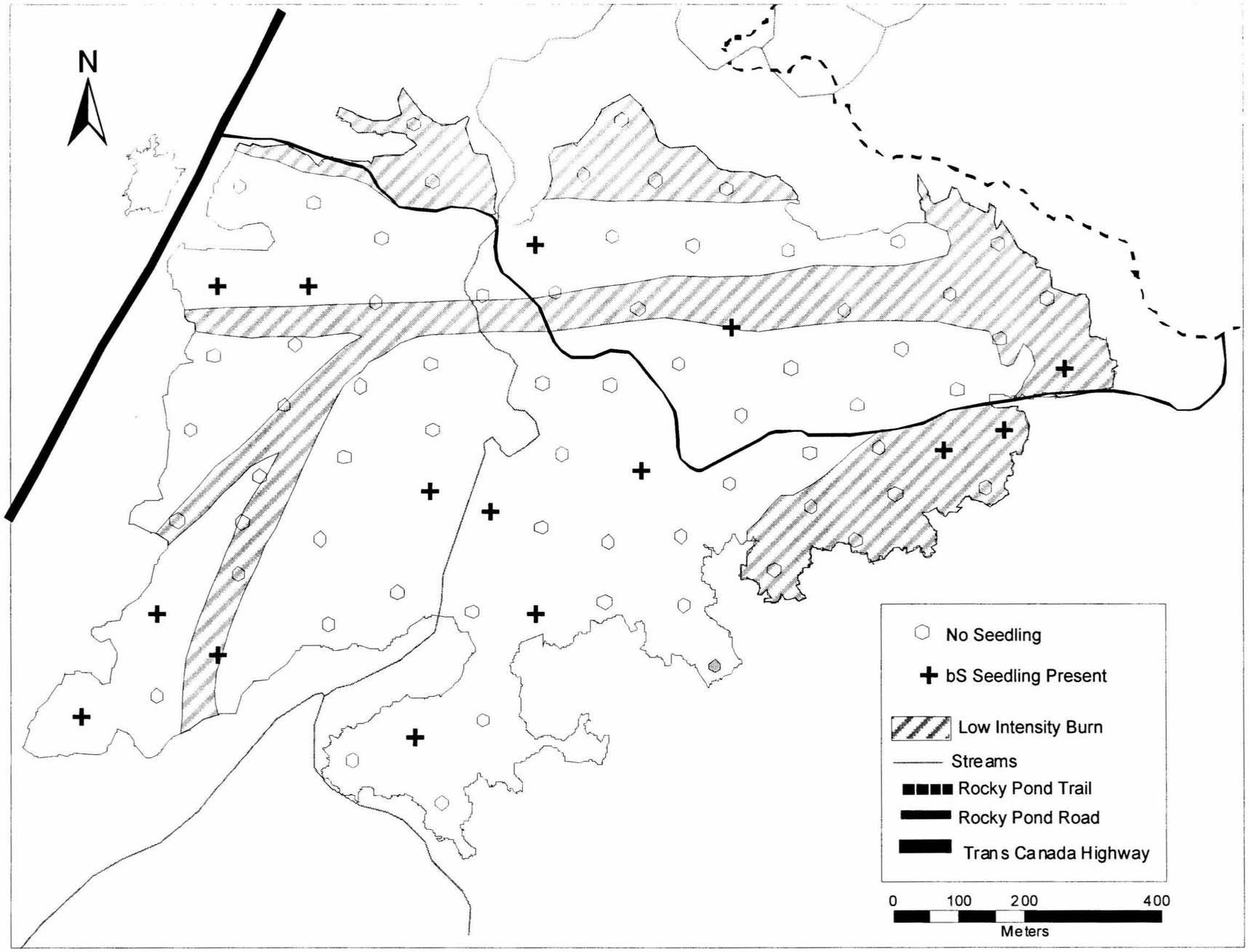

Figure 13. Map of seedling distribution as identified in 1x1 metre survey at each sampling point within the burn perimeter.

3.4 CLIMATE AND MICROCLIMATE

In analysis of soil moisture (at 10 cm) for the four seedbeds and for burn intensity, the interaction between the two effects was significant so the two intensities were analysed separately. Soil moisture among the four seedbeds was significantly different within both the low-intensity burn ($F_{[3, 68]} = 66.7$, $p < 0.0001$) and the high-intensity burn ($F_{[3, 68]} = 2113$, $p < 0.0001$). The range for soil moisture was considerably higher in the low intensity burn (Figure 14). The largest difference was attributed to moisture below the lichen mat, with a higher average value (0.436 m^3/m^3) for the low-intensity burn compared with only (0.066 m^3/m^3) for the high-intensity burn.

The 2003 growing season in TNNP was warmer and drier than normal (Table 10). Total precipitation for the summer (including October) was 492.3 mm compared to the total mean monthly value of 572.0 mm. Temperatures during the growing season were above normal, and surface temperatures at the burn site reached maximum values between 35.3 and 35.7 °C. Mean growing degree-days (GDD) above 5 °C were 1643 for 2003 compared with a mean of 1263 (Figure 15), due to above average daily minimum and maximum temperatures for September and October and an extended frost free autumn. This resulted in continued emergence and ultimately death of some experimental seedlings in late October.

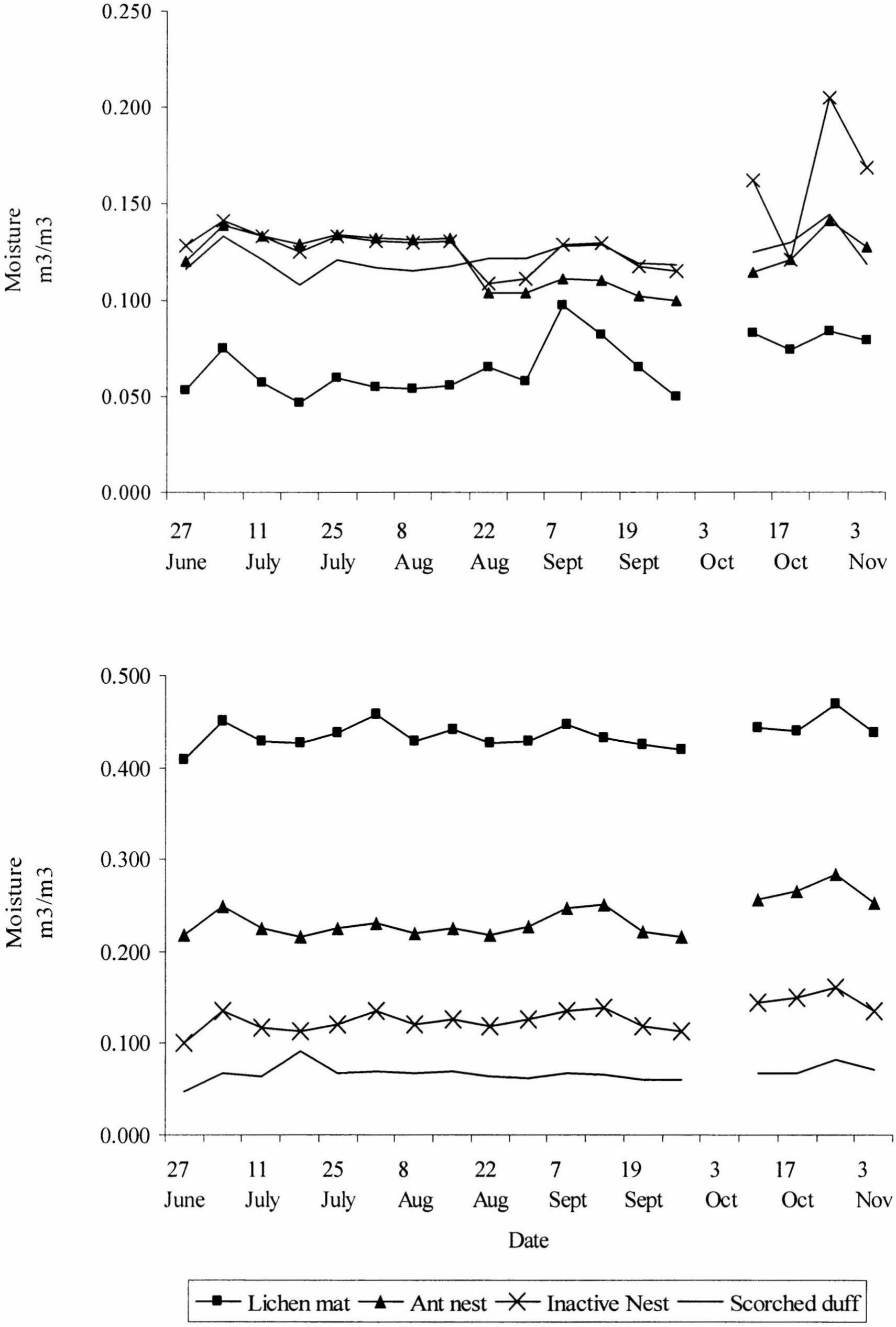

Figure 14. Soil moisture (m^3/m^3) at 10 cm depth for the four types of seedbed for the high-intensity burn (top) and the low-intensity burn for the period 27 June to 03 November (no data collected on 03 October).

Table 10. Climate Normals (1971-2000) for Terra Nova National Park from May through October compared with 2003 values.

	May		June		July		August		September		October	
	Mean	2003	Mean	2003	Mean	2003	Mean	2003	Mean	2003	Mean	2003
Daily Max (°C)	11.9	15.2	17.1	20.3	21.4	24.5	21.0	23.1	16.4	21.5	10.2	15.9
Daily Min (°C)	2.2	2.4	6.5	6.6	10.8	13.2	11.2	11.7	7.6	11.1	2.8	7.7
Daily Mean (°C)	7.0	5.7	11.8	12.4	16.1	17.8	16.1	17.2	12.0	15.8	6.5	11.4
GDD Above 5°C	90	45	206	253	344	419	339	379	211	339	73	208
Precip (mm)	87.6	94.4	88.2	42.1	88.3	63.6	88.7	55.5	108.6	55.7	110.6	181.0

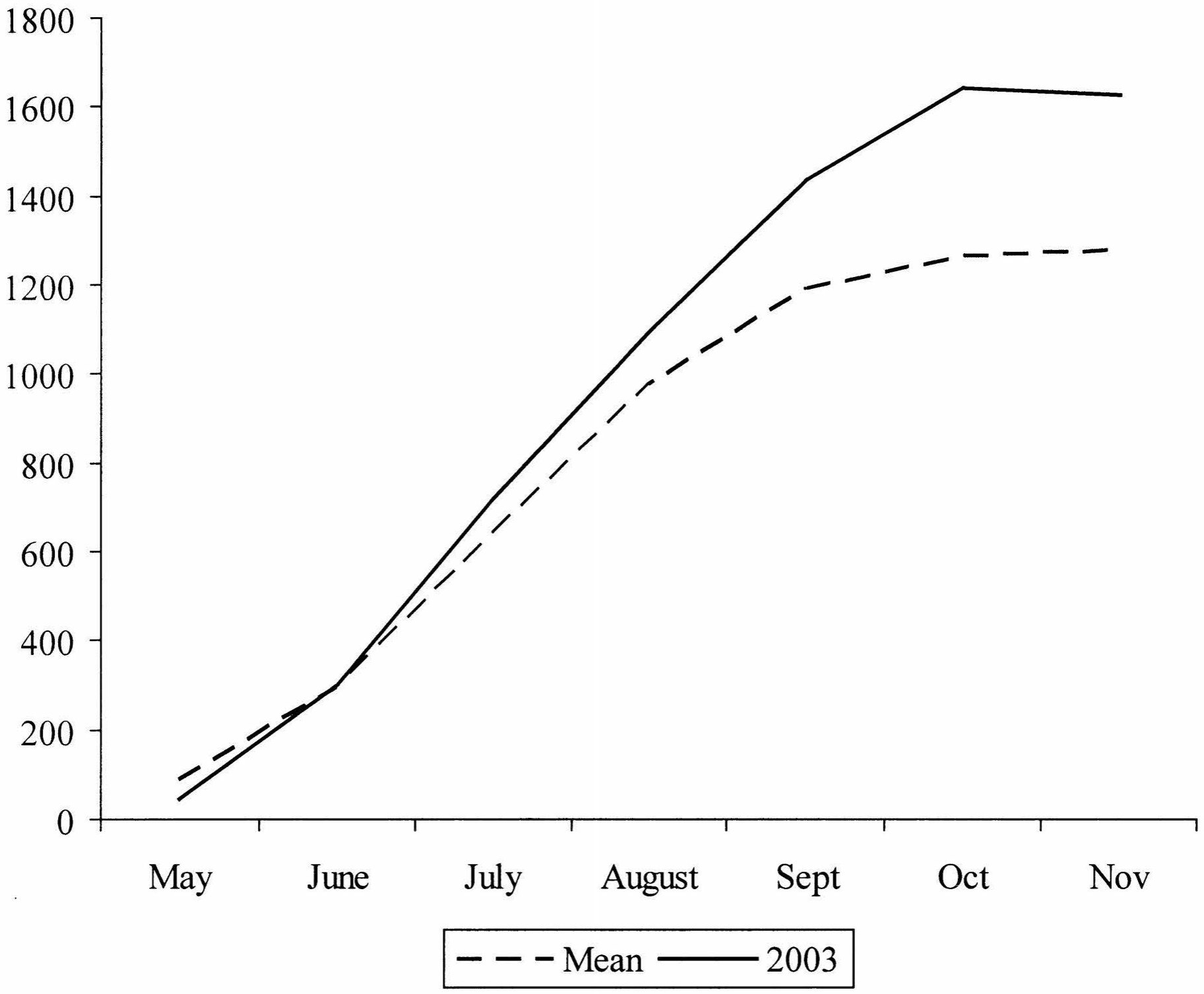

Figure 15. Mean (1971 – 2000) cumulative growing degree days above 5(C compared with 2003 values.

CHAPTER 4: DISCUSSION

Seed fell throughout most of the burned area and approximately 1 476 500 black spruce seeds per ha were released from trees in and around the burn, a number within the range of dispersal described for this species (Viereck and Johnston, 1990). Given that only 8.9% of all sampled black spruce throughout the burned area contained cones, with a mean of 23.8 cones per tree and assuming only 2.2 to 3.7 filled seeds per cone (Schooley *et al.*, 1979), then 15 289 to 25 714 seeds per ha would have fallen. Since a total of 1 476 500 black spruce seeds per ha was estimated, there are three possible conclusions: that a high number of the seeds disseminated from the burn edge, that a majority of the seeds actually fell before the fire and were not destroyed, or a combination of both. If seeds were present on the ground prior to the fire, they likely would not have contributed much to post-fire regeneration. Once dispersed, spruce seeds remain viable for only a short period and on a natural forest floor seedbed, black spruce seeds lose viability after16 months (Fraser, 1976). Given the black spruce seed estimate of 16 539 per ha from 2003 seed trap data and the number and condition of cones, trap data more accurately reflects annual post-fire input of seed and duff cores represent an accumulation of pre-fire seed on the ground over time.

Seed-bearing duff cores were found throughout the burn, and the traps captured more seed at the forest edges and in low-intensity burn areas. Throughout the burn, many cones were damaged or were destroyed by fire and most collected cones contained no seed. These findings highlight the importance of seed trees located at burn edges.

Undamaged trees in unburned patches are even more important for post-fire black spruce regeneration, as in spite of their light weight and relatively large wings, black spruce seeds are not commonly dispersed over long distances. Wind dispersal is effective up to <100 m from the windward edge of a stand (Viereck and Johnston, 1990; Johnston *et al.*, 1983), although this distance was given for higher-density black spruce stands. Hence, the centres of large burns are usually slow to regenerate and the establishment of widely scattered black spruce seedlings in a post-fire area are important as future seed sources (Foster, 1985). For the low density lichen-woodland, they are even more important.

The reduction in canopy seed banks by squirrel predation affected the role of edge trees for stand regeneration. In Newfoundland, the proportion of black spruce cones per tree harvested by red squirrels in years with small cone crops has ranged from 64 to 96% (West 1989). In this study, squirrels removed up to 100% of the cones on some trees with a mean removal percentage of just over 50%. The percentage of filled (viable) seed per hectare remaining for dispersal after red squirrel predation in eastern Newfoundland was reported as low as 0% on some black spruce sites in 2001 and anywhere from 7% to 58% in 2002 (Tulk, 2004). That study also demonstrated that seed discarded by red squirrels at feeding sites was of low viability, suggesting that the most viable seed was the target of predation. The negative impact on seed quality and quantity by squirrels is certain, but the effect on forest succession is less clear. Black spruce stands severely damaged by spruce budworm (*Choristoneura fumiferana* (Clem.)) may already have a low seed bank, which would impair post-fire regeneration (Simard and Payette, 2001). It has been suggested that the impact of spruce budworm on vegetative buds, combined with the

effects of fire may actually account for the presence of low-latitude lichen woodland (Payette *et al.*, 2000). In spite of the fact that budworm still persists at varying levels in TNNP and that squirrel densities are high, the amount and extent of seed rain indicates no large-scale negative impact to post-fire regeneration due to predation by squirrels or budworm. Although these factors may not affect the re-establishment of the low density lichen woodland community, their impact in limiting seed source for establishment of a higher density black spruce forest on this site is certainly possible.

The pattern of fire severity observed was as predicted for this forest type, it being greatest in areas occupied by black spruce clumps (Bloom, 2002; Treter, 1995; Alexander *et al.*, 1991; Day, 1982). This greater severity was the result of a higher amount of combustible material, hence a longer duration of burn (Alexander *et al.*, 1991). Smouldering fires persisted under tree crowns where vegetation was rich in mosses, where organic soil layers were deeper (Treter, 1995) and where tree branches covered the ground (Bloom, 2002; Day, 1982). In the high-intensity fire, smouldering combustion and therefore duff reduction was greater. Areas experiencing high-intensity fire were those in the path of the flaming front, resulting in higher temperatures and greater fuel consumption. Low-intensity fire effects resulted from burning at the rear and flanks (sides) of the fire. Regardless of fire intensity, the reduced duff depth provided a possibility for seed germination, even though the fire did not burn away the entire duff layer to expose mineral soil. During the first season of growth, the roots of emerging black spruce seedlings elongate ≤ 2 cm (Foster, 1985; Heinselman, 1957), making regeneration from seeds better in areas with a relatively shallow organic layer

(Richardson, 1970). Both seeded and naturally occurring black spruce seedlings were initially able to take advantage of the newly created micro-sites in the TNNP fire. However, areas of high-severity burn did not necessarily provide safe sites for establishment. The blackened and porous nature of scorched duff usually results in highly fluctuating temperature and moisture regimes (Foster, 1985; Kilgore, 1985; Kershaw, 1977), which may cause complete germination failure even with a sufficient seed source (Place, 1955). There have been reported increases in soil temperatures of 60-70% in blackened soil (Rouse, 1976). As a consequence of temperatures produced in direct sunlight (Vincent, 1965), scorched duff is an unfavourable seedbed, with seedling mortality often highest on this substrate (Sirois, 1993; Viereck and Johnston, 1990). With extreme high daily temperatures recorded at the surface, drought-caused seedling mortality was prevalent in both this and another concurrent study at the Rocky Pond site (Moss, 2004). In that case, most spruce seedling mortality was due to drought rather than other factors such as predation by invertebrates. The majority of deaths occurred in the high-intensity burn areas, a factor attributed to lack of shading (Moss, 2004). In summary, areas of high-severity burn allowed for seedling germination but rarely provided safe sites for establishment.

Seed germination was not entirely restricted by the presence of the lichen mat in this study. Although lichen itself is a poor seedbed for spruce due to its extreme and rapid fluctuations in moisture content (Foster, 1985; Richardson and Hall, 1973), observations from this study confirmed that in all cases - seeding trial or natural seedlings - successful germination in the lichen layer occurred in desiccation fractures, a phenomenon

previously reported (Lafleur *et al.*, 2002; Sirois, 1993). Seeds falling into cracks in the lichen layer, which maintains soil moisture near field capacity, may lead to germination, growth and survival on soils that would otherwise be too dry (Kershaw, 1977). Although it is possible that seed germination may occur in the lichen mat in mature and older lichen-woodland stands (because desiccation fractures also occur there), the thickness of the lichen layer would likely limit access to the soil below (Bonan and Shugart, 1989; Kershaw, 1977). In this study the lichen layer in the unburned condition was found to average 12.5 cm (maximum 19 cm) in depth. With reduction in lichen depth by as much as 88% by fire, the possibility for seed germination in the layer was greatly enhanced.

It is difficult to attribute the difference in ant nest density to fire effects, in spite of the sizeable disparity between burned and unburned areas. Differences may have been due to location, as the unburned portion of lichen woodland had a higher forest edge to area ratio (0.022 VS 0.011). With the exception of carpenter ants (*Camponotus herculeanus* L.), which were collected from a decaying log, all ant specimens identified belonged to the species group *Formica fusca* L. (Larson, pers. comm. 2001). This native species inhabits ground nests in open, unshaded areas (Hölldobler and Wilson, 1990). Ant activity was high in the burned area throughout the study period. Ants function more efficiently in higher temperatures (above 20°C) (Hölldobler and Wilson1990) but the lichen layer keeps underlying soil cool and moist (Bonan and Shugart, 1989; Kershaw, 1977). The reduction in lichen depth and creation of heat absorbing charred organic soil (Foster, 1985; Kilgore, 1985; Kershaw, 1977), caused higher soil temperatures in the burned area, likely leading to increased ant activity and to nest expansion. However,

measurements did not show a statistically significant difference in mean nest size between the burned and unburned areas. It is possible that ant activity is not resulting in larger nests, but is directed towards building new nests, or abandoning and re-building the same nests.

Noteable in this study area is the extremely high nest numbers recorded. In the Parc des Grands-Jardins (PGJ), Québec, the total area occupied by ant nest mounds in a similar lichen-spruce woodland was relatively small (Lafleur *et al.*, 2002). There, an average surface area of 0.25 m^2 per nest mound and a total surface area exposed by mounds of 20 m^2 per ha, or 0.2% of their 80 ha study area was estimated. In contrast, this study reports twice the average nest size in the burned area and 314 m^2 per ha of total surface area covered by ant nests. This is 3.2% of the 98 ha burned area and 16 times greater than the estimate in the PGJ. However, the relatively large portion of mineral soil exposed due to ant activity did not appear to translate to increased available seedbed for spruce.

Although seedling emergence was highly variable for the seedbeds in this study, one constant in the seeding trial was that no seedlings germinated on any active ant nests in any of the plots. This supported earlier findings (Lafleur, *et al.*, 2002). There are many documented cases of ant effects on seed (e.g. Hölldobler and Wilson, 1990; Andersen and Ashton, 1985; Culver and Beattie, 1983). However, it remains unknown in this case whether ants directly impact black spruce seed through predation, removal or burial. Observations made throughout the course of this investigation suggest that growth of nest mounds is constant, with worker ants moving material to reinforce and repair nests. This

activity could have resulted in seeds at the surface becoming buried too deep for germination, or removed from the surface. Still, soil properties of the nest mounds were likely not suitable for germination or survival (Lafleur *et al.*, 2002). Nests were found to be extremely dry to the touch at or just below the surface, even during and after periods of rainfall. The few natural seedlings that were discovered growing on active ant nests were discovered at a nest perimeter.

Germination failure was consistent for active nests, but the seeding trial demonstrated that germination could occur on abandoned ant nests. This phenomenon, on first observation, is contrary to earlier findings where no black spruce seedlings were found near active or abandoned nest mounds in Quebec (Lafleur *et al.*, 2002). In addition to the lack of active soil movement by ants, soil moisture was higher at the surface and soil structure less porous in ant nests after they were abandoned. However, while moist mineral soils usually provide good seedbeds for black spruce, exposed mineral soil may be subject to frost heaving in low-lying areas and in the case of coarse sands, prone to drought (Jeglum, 1979; Vincent, 1965). This, was found to be the case in TNNP. Initial survival in the first growing season for the abandoned nests was high (89%), but only four out of nine seedlings survived the first winter (2003-2004). Hence, the low occurrence of natural seedlings in this substrate may not have been caused by germination failure but by poor initial survival in frost or drought conditions.

The low response of the experimental seedlings resulted in an analysis with insufficient power; therefore the results of the study make it difficult to statistically declare a seedbed preference for black spruce. However, soil moisture appears to be a key

limiting factor for germination success in the lichen woodland of TNNP and other locations (Sirois and Payette, 1991; Sirois and Payette, 1989; Foster, 1985; Thomas and Wein, 1984; Heinselman, 1981; Kershaw, 1977). While the germination of seedlings was highly variable in three of the four seedbeds studied, there was a constant moisture supply at some of the study sites and thus a positive germination response in all three seedbed types.

At present, pre- and post-fire stand structure appears comparable. After two seasons, the density of naturally regenerating seedlings is 524 per ha, indicating that early recruitment is at a density of only 11.5% of the original stand (4573 stems per ha). Yet, each seedling, through future vegetative layering, will likely be the origin of a new spruce clump. Taking early recruitment as a minimum, the resultant number of clumps per ha would then be greater when compared to the original number (445 clumps per ha). The original stand had an average of 9 stems per clump, which, if the new stand followed a similar pattern of vegetative propagation, would increase stem density to 4716 per ha compared to the original 4573 stems per ha. However, taking into account a minimum of 50% cone removal by squirrels, then twice the number of seeds per hectare should have fallen. It is possible that future stand density could have been as high as 9432 stems (and subsequently clumps) per ha, significantly higher than the seedling density of 2500 per ha considered optimal (Viereck and Johnston, 1990). In either case, future stand density will not be uniform, at least initially, as revealed by the arrangement of seedlings after the first two growing seasons (Figure 18).

The effect of the seedbed limiting lichen mat masks the assessment of the various other impacts on forest succession. The post-fire density of the lichen woodland is usually low compared to the optimal density for black spruce. Post-fire densities of 429 seedlings per ha in lichen woodland communities in central Newfoundland (Richardson and Hall, 1973) and densities of between 320 and 4670 per ha in Labrador (Treter, 1995) have been reported. A density of 3-4 seedlings per m^2 (30 000 – 40 000 per ha) is considered adequate stocking for regenerating black spruce stands (Greene *et. al.*, 1999; Viereck and Johnston, 1990). Since the lichen mat reduces seedling establishment (Morneau and Payette, 1989), seedling densities will be low regardless of large inputs of seed (Arseneault, 2001; Payette *et al.*, 2000; Sirois, 1995; Sirois, 1993; Sirois and Payette, 1991; Sirois and Payette, 1989). Low seedling and stand density after fire may be a result of a low number of viable seeds. However, using seed input assessed from trap data to evaluate the regenerative capacity of the stand, it is unlikely. The total seed released after the 2002 fire is unknown, but even if the value from 2003 (16 539 seeds/ha) is doubled to reflect both years (total of 33 078 seeds/ha), then 524 seedlings/ha/33 078 seeds/ha = 1.58%. This value closely resembles the 1.5% of the seeding trial (with seed viability of 90%). In all likelihood, this seed fall estimate is conservative and viability was much lower. Past studies have reported low viability rates: 0-21.4% (Sirois, 1995), 0.2% to 1.8% (Zasada *et al.*, 1979) and between 0% and 19% (Wein, 1975). However, the conclusion is that much surviving seed was viable and that low numbers of seedlings were predominantly due to lack of suitable seedbed.

The extensive cover of *Kalmia angustifolia* on this site may be a compounding factor, as it has been reported as an inhibitor for black spruce regeneration for various reasons such as allelopathic inhibition (Zhu and Mallik, 1994; Mallik and Newton, 1988; Mallik, 1987), immobilization of soil nitrogen in living and dead Kalmia biomass (Mallik, 1996), creation and/or acceleration of iron pan formation (Damman, 1970) and the creation of a thick duff layer (Mallik, 1989). However, in the case of the recently burned lichen woodland, the initial re-sprout density of *Kalmia* is low (Hermanutz, 2005) and unlikely to inhibit early black spruce seedling germination. In addition, relative to the inhibitory effects of the extensive lichen mat, its effects would be much smaller in proportion. The impact of *Kalmia* on future growth of black spruce would need to be investigated.

An important consideration in determining future stand density is the potential for future seedling recruitment. There have been varied reports on the timing of black spruce seedling establishment after fire. Wein (1975) reported peak establishment occurs two to three years after fire and ceases by the sixth year. Charron and Greene (2002) also reported a peak in age structure of black spruce seedlings in the second year following fire. Other studies indicate that tree recruitment takes place within a short (3 to 10 year) period after fire (Johnstone, *et al.*, 2004; Greene and Johnson, 1999). In northern Quebec, the black spruce establishment stage was reported to span a 20-30 year period before the local seed supply was exhausted (Morneau and Payette, 1989; Sirois and Payette, 1989). However, it was suggested that the large span of stand ages recorded was possibly due to age underestimation (Sirois and Payette, 1989) and recent studies have demonstrated this

miscalculation (Parisien, *et. al*., 2005; DesRochers and Gagnon, 1997), leading to the conclusion that post-fire black spruce stand initiation takes place in a much shorter time-frame. In the Rocky Pond fire, the majority of seedlings observed during surveys germinated in 2003, the second full growing season following the fire. It remains to be seen, with on-going impacts on seed, whether or not seedling establishment continues and what its rate will be.

The long term survival of black spruce seedlings in the TNNP lichen-woodland into the future is yet to be determined, but climate will likely be critical in the early stages of establishment. The summer of 2003 was very dry with higher than normal temperatures – conditions that are amplified on an extremely dry site, as is the case with the TNNP lichen woodland. Also, the extended growing season of that year resulted in some germination occurring in the fall, when many of these late seedlings succumbed to frost. This would have served to reduce the amount of viable seed for germination in the following season. As noted, early post-fire regeneration is usually low in a lichen-spruce woodland (Morneau and Payette, 1989; Sirois and Payette, 1989; Foster, 1985), likely a reflection of poor seedling survival (Charron and Greene, 2002) more so than problems of seed crop, seedbeds, or seed viability. However, the initial and continued impact of predation by squirrels cannot be discounted. Thus, the next few years will be critical in determining if the recently burned lichen woodland in TNNP will undergo succession like that described elsewhere and that has occurred previously in TNNP (Lavoie and Sirois, 1998; Sirois, 1995; Treter, 1995; Sirois and Payette, 1989; Dyrness *et al.*, 1986; Foster, 1985; Kershaw, 1977 (Figure 16). Monitoring will determine the importance of

the earliest seedlings in terms of survival, the extent of continuing seed rain into the burned area, the continuation or cessation of seedling establishment and their combined effect on community succession and structure.

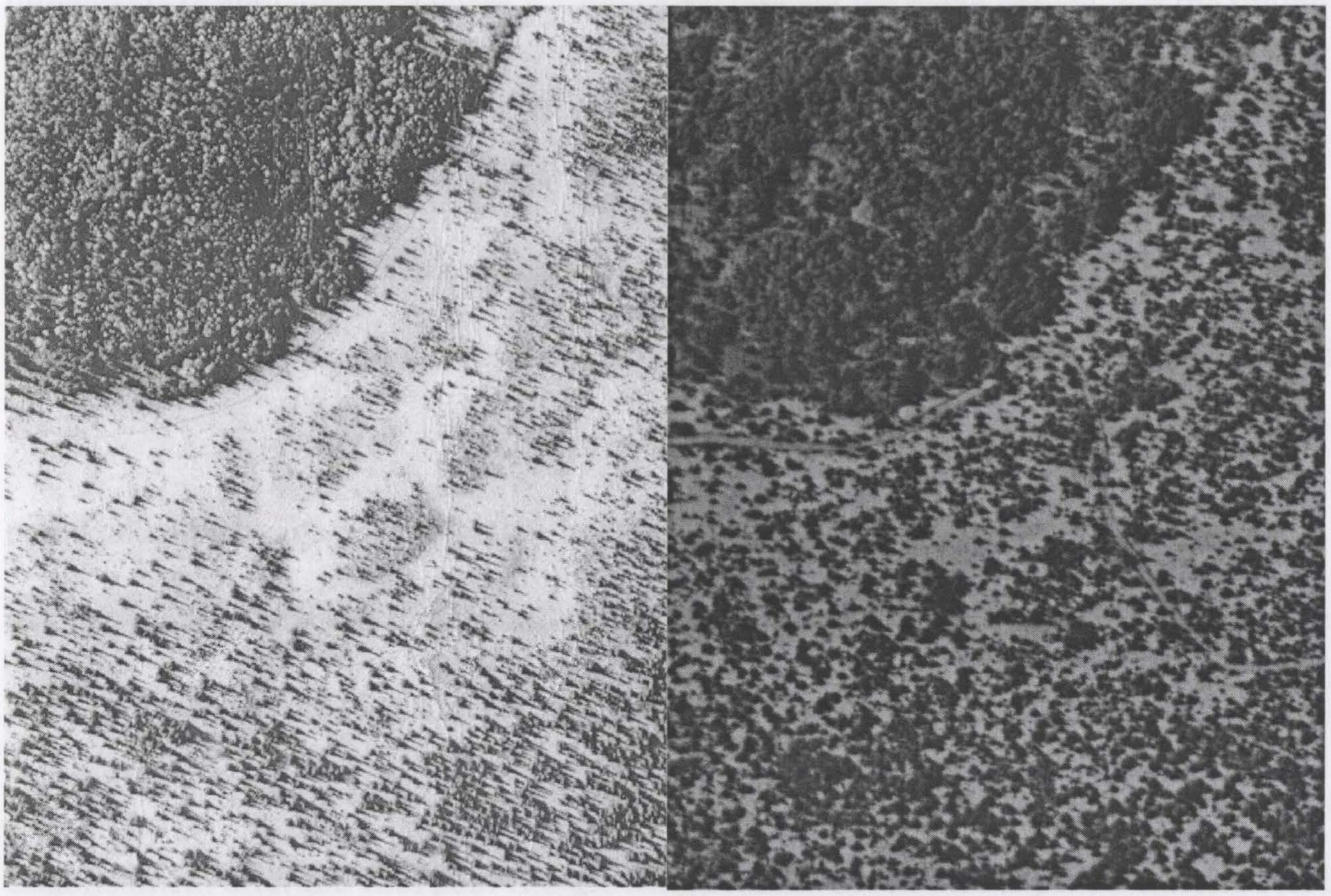

Figure 16. Portions of air photographs of the same location of the lichen woodland in TNNP (1:12 500 scale) taken in 1960 (left) and 1996. The higher density depicted in the recent photo indicates clump expansion due to layering and additional, though likely much less, recruitment from seed.

CHAPTER 5: CONCLUSIONS

The Rocky Pond fire burned severely enough, regardless of fire intensity, to prepare seedbeds for black spruce germination. The results of this study made it impossible to statistically declare a seedbed preference for black spruce, but the timing of observations of germination and mortality was important for understanding seedling patterns and drawing conclusions on seedbed preference. Soil moisture appears to be a key limiting factor for germination success. Seedling mortality was highest on the charred, blackened organic soil substrate under former spruce canopies. Seed germination was not entirely restricted due to the presence of caribou lichen and black spruce seeds could take advantage of dessication fractures in the lichen cover. Nonetheless, the extensive lichen mat did limit seedling establishment and low numbers of seedlings were predominantly due to lack of available seedbed. The presence of abandoned ant nests produced a seedbed that likely increased seed germination, but did not result in seedling establishment after the first post-fire growing season. Given that exposed mineral soil is prone to drought and frost heaving, the amount of available seedbed for successful black spruce establishment may actually be reduced by the presence of the abandoned nests. Active nests were completely unsuitable for germination. It is yet to be determined if the ants themselves have any direct effect on seedling recruitment (e.g. predation) aside from effects via altered soil properties.

There appears to be sufficient post-fire seed rain in order to re-establish low-density lichen woodland. However, the impact of predation by red squirrels in limiting seed source for establishment of a higher density black spruce forest on the site is

possible. In addition, extremes in climate during the first critical years of post-fire establishment can and will have an impact on succession of very dry sites. Continued monitoring can determine the importance of the seedlings established in the first few years following fire in perpetuating the lichen woodland. Such monitoring must include measures of seedling survival, the extent of continuing seed rain on the burned area, the continuation or cessation of seedling establishment and their combined effects of all these factors on community succession and structure.

LITERATURE CITED

Alexander, M. E. 1982. Calculating and interpreting forest fire intensities. *Canadian Journal of Botany* 60: 349-357.

Alexander, M. E., Stocks, B.J. and B.D. Lawson. 1991. Fire behavior in black spruce-lichen woodland: the Porter Lake Project. Forestry Canada, Northern Forestry Center Information Report. NOR-X-310. 44 pp.

Allan, T. 1997. *Kalmia angustifolia* vegetation dynamics and black spruce regeneration after natural Fires. Unpublished Honours Thesis. Lakehead University. 34 pp.

Andersen, A. N. and D. H. Ashton. 1985. Rates of seed removal by ants at heath and woodland sites in southeastern Australia. *Australian Journal of Ecology* 10: 381-390.

Arseneault, D. 2001. Impact of fire behavior on postfire forest development in a homogeneous boreal landscape. *Canadian Journal of Forest Research* 31: 1367-1374.

Auclair, A. N. D. 1983. The role of fire in lichen-dominated tundra and forest tundra. *In* The Role of Fire in Northern Circumpolar Ecosystems. *Edited by* R.W. Wein and D.A. MacLean. John Wiley & Sons Ltd. pp 235-256.

Bloom, R. 2002. Direct and indirect effects of post-fire conditions on successional pathways and ecological processes in black spruce-*Kalmia* forests. Unpubl MSc. Thesis. Lakehead University, Thunder Bay, Ontario. 188 pp + iv.

Bonan, G. B. 1989. Environmental factors and ecological processes controlling vegetation patterns in boreal forests. *Landscape Ecology* 3: 111-130.

Bonan, G. B. and H. H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics* 20: 1-28.

Byram, G. M. 1959. Combustion of forest fuels. *In* Forest Fire: Control and Use. *Edited by* K.P Davis. McGraw-Hill, New York. pp. 61-89.

Charron, I. and D. F Greene. 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. *Canadian Journal of Forest Research* 32: 1607-1615.

Culver, D. C. and A. J. Beattie. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado montane meadow. *Ecology* 64: 485-492.

Damman, A. W. H. 1970. Effects of vegetation changes on the fertility of a Newfoundland forest site. *Ecological Monographs*.41: 252-270.

Damman, A. W. H. 1983. An ecological subdivision of the island of Newfoundland. *In* Biogeography and ecology of the island of Newfoundland. *Edited by* G. R. South. Junk Publishers. The Hague, The Netherlands. 723 pp.

Dauber, J. and V. Wolters. 2000. Microbial activity and functional diversity in the mounds of three different ant species. *Soil Biology and Biochemistry* 32: 93-99.

Day, R. T. 1982. The vegetation and organic soil layer in *Kalmia*-spruce postfire communities. Unpublished MSc. Thesis. University of New Brunswick, Fredericton, New Brunswick. 69 pp + ix.

DesRochers, A. and R. Gagnon. 1997. Is ring count at ground level a good estimation of black spruce age? *Canadian Journal of Forest Research* 27: 1263-1267.

Dyrness, C. T., Viereck, L. A. and K. Van Cleve. 1986. Fire in taiga communities of interior Alaska. *In* Forest Ecosystems in the Alaskan Taiga. *Edited by* K. Van Cleve. Springer-Verlag New York, Inc., New York U.S.A. pp 74-85.

English, B. 1998. Impact of squirrel predation on white pine cone collection efforts in Newfoundland. Silviculture Notebook(42). Newfoundland Forest Service. 4 pp.

Environment Canada, Meteorological Service of Canada. 2001. 30-year climate normals 1971-2000. On-line data http://www.climate.weatheroffice.ec.gc.ca (accessed August 2004).

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7: 1221-1244.

Foster, D. R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of southeastern Labrador, Canada. *Journal of Ecology* 73: 517-534.

Fraser, J. W. 1976. Viability of black spruce seed in or on a boreal forest seedbed. *Forestry Chronicle* 52: 229-231.

Greene, D. F. and E.A. Johnson. 1999. Modelling recruitment of *Populus tremuloides*, *Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. *Canadian Journal of Forest Research* 29: 462–473.

Greene, D. F., Zasada, J. C., Sirois, L., Kneeshaw, D. Morin, H., Charron, I. and M.-J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research* 29: 824–839.

Heinselman, M. L. 1957. Sylvical characteristics of black spruce (*Picea mariana*). U.S. Dept. Agric., For. Serv., Lake States Forest Experimental Station Paper 45.

Heinselman, M. L. 1981. Fire and succession in the conifer forests of northern North America. *In* Forest succession: concepts and applications. *Edited by* D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag New York, Inc., New York U.S.A. pp 374-405.

Hermanutz, L. 2005. Unpublished data. Boreal Ecology class, Department of Biology, Memorial University of Newfoundland. St. John's, Newfoundland and Labrador.

Herr, D. G. and L. C. Duschene.1995. Jack pine (*Pinus banksiana*) seedling establishment is affected by organic horizon removal, ashes, soil, water and shade. *Water, Air & Soil Pollution* 82: 47-154.

Hölldobler, B. and E. O. Wilson. 1990. The Ants. Cambridge, Mass. Belknap Press of Harvard University Press. Cambridge, Mass. 732 pp + xii.

Jeglum, J. K. 1979. Effects of some seedbed types and watering frequencies on germination and growth of black spruce: a greenhouse study. Canadian Forestry Service, Report O-X-292. Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario. 33 pp.

Johnston, W. F., and T. M. Smith. 1983. Black spruce. *In* Silvicultural systems for the major forest types of the United States. Russell M. Burns, tech. comp. U.S. Department of Agriculture, Agriculture Handbook 445. Washington, DC. pp. 96-98.

Johnstone, J. F., Chapin, F.S, Foote, J., Kemmett, S., Price, K. and L. Viereck. 2004. Decadal observations of tree regeneration following fire in boreal forests. *Canadian Journal of Forest Research* 34: 267-273.

Kershaw, K. A. 1977. Studies on lichen-dominated systems. XX. An examination of some aspects of the northern boreal lichen woodlands in Canada. *Canadian Journal of Botany* 55: 393-410.

Kilgore, B. M. 1985. The role of fire in wilderness: A state-of-knowledge review. Proceedings - National Wilderness Research Conference, July 23-26, 1985. US Forest Serv. 72 pp.

King, R. L. 1977. The plant ecology of anthills in calcareous grasslands: I: patterns of species in relation to anthills in southern England. *Journal of Ecology* 65: 235-256.

Laakso, J. 1999. Short-term effects of wood ants (*Formica aquilonia* Yarr.) on soil animal community structure. *Soil Biology and Biochemistry* 31: 337-343.

Laakso, J. and H. Setälä. 2000. Impacts of wood ants (*Formica aquilonia* Yarr.) on the invertebrate food web of the boreal forest floor. *Annales Zoologici Fennici* 37: 93-100.

Lafleur, B., Bradley, R. L., and A. Francoeur. 2002. Soil modifications created by ants along a post-fire chronosequence in lichen-spruce woodland. *Écoscience* 9: 63-73.

Larson, D. 2001. Family *Formicidae* – Unpublished Checklist of Newfoundland species. Department of Biology, Memorial University of Newfoundland. St. John's, Newfoundland and Labrador.

Lavoie, L. and L. Sirois. 1998. Vegetation changes caused by recent fires in the northern boreal forest of eastern Canada. *Journal of Vegetation Science* 9: 483-492.

Lenoir, L., Persson, T., and J. Bengtsson. 2001. Wood ant nests as potential hot spots for carbon and nitrogen mineralisation. *Biology and Fertility of Soils* 34: 235-240.

Linehan, B. 2003. Personal Communication. Provincial Tree Nursery, Newfoundland and Labrador Department of Forest Resources, Woodale, Newfoundland and Labrador.

Mallik, A. U. 1987. Allelopathic potential of Kalmia angustifolia to black spruce (*Picea mariana*). *Forest Ecology and Management*. 20: 43-51.

Mallik, A. U. 1989. Inhibitory effects of water leachates of Kalmia angustifolia and forest organic matter on softwood seedlings. Unpubl. Rept., Canadian Forestry Service, St. John's, NF. 19 pp.

Mallik, A. U. 1996. Effects of natural fires on vegetation structure, composition and soil properties of selected forest sites of Terra Nova National Park, Newfoundland: A preliminary study. Department of Biology, Lakehead University, Thunder Bay, ON. 23 pp + iii.

Mallik, A. G. and P. F. Newton. 1988. Inhibition of black spruce seedling growth on the forest floor substrates of central Newfoundland. *Forest Ecology and Management*. 23: 273-283.

Medina, E. and J. F. Silva. 1990. The savannas of northern South America: a steady regulated by water-fire interactions on a background of low nutrient availability. *Journal of Biology* 17: 403-413.

Motulsky, H. 1995. Intuitive Biostatistics. Oxford University Press, New York. 386 pp.

Morneau, C. and S. Payette. 1989. Post-fire lichen-spruce woodland recovery at the limit of the boreal forest in northern Québec. *Canadian Journal of Botany* 67: 2770-2782.

Moss, M. 2004. The impact of slug herbivory on post-fire regneration of black spruce in lichen woodland in Terra Nova National Park, NL. Unpublished MES Thesis. Memorial University of Newfoundland, St. John's, Newfoundland and Labrador. 43 pp.

Nelder, J. A. and R. W. M. Wedderburn. 1972. Generalized linear models. *Journal of the Royal Statistical Society, Series A* 135: 370-384.

Nguyen-Xuan, T., Bergeron, Y., Simard, D., Fyles, J.W., and D. Paré. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. *Canadian Journal of Forest Research* 30: 1353-1364.

Nkem, J. N., Lobry de Bruyn, L. A., Grant, C. D. and N. R. Hulugalle. 2000. The impact of ant bioturbation and foraging activities on surrounding soil properties. *Pedobiologia* 44: 609-621.

Parisien, M., Sirois, L. and S. Parent. 2005. Landscape-level variability in the age underestimation of understory black spruce in the northern boreal forest of Quebec *Canadian Journal of Forest Research* 35: 633–642.

Payette, S., Bhiry, N., Delwaide, A., and M. Simard. 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce-moss forest. *Canadian Journal of Forest Research* 30: 288-305.

Payne, N. F. 1976. Red squirrel introduction to Newfoundland. *Canadian Field Naturalist* 90: 60-64.

Place, I. C. M. 1955. The influence of seedbed conditions on the regeneration of spruce and balsam fir. Canadian Dept. of Northern Affairs & Natural Resources, Forest Branch Bulletin 117.

Power, R. G. 1996. Forest Fire History and Vegetation Analysis of Terra Nova National Park. Parks Canada Technical Reports in Ecosystem Science. 40 pp. + ix.

Power, R. G. 2000. Vegetation Management Plan for Terra Nova National Park: 2000-2004. Terra Nova National Park. Parks Canada Agency. 99 pp + viii.

Reynolds, J. J. 1997. Population ecology, home range size, and caching behaviour or red squirrels (*Tamiasciurus hudsonicus*) in Terra Nova National Park, Newfoundland. Unpublished MSc. Thesis. Memorial University of Newfoundland, St. John's, Newfoundland and Labrador. 95 pp + xi.

Richardson, J. and J. P. Hall. 1973. Natural regeneration after disturbance in the forests of Central Newfoundland. Can. Forest Serv., Information Report N-X-86. 62 pp.

Richardson, J. 1970. Broadcast seeding a burned cutover after light scarification. Canadian Forest Service, Information Report N-X-58. 21 pp.

Rouse, W. R. 1976. Microclimatic changes accompanying burning in subarctic lichen woodland. *Arctic and Alpine Research* 8: 357-376.

Rowe, J. S., Spittlehouse, D., Johnson, E., and M. Jasieniuk. 1975. Fire studies in the upper Mackenzie Valley and adjacent Precambrian Uplands. Canadian Department of Indian Affairs and Northern Development, ALUR Rep. 74-75-61. 128 pp.

Rowe, J. S. 1972. Forest Regions of Canada. Forest Service Publication No. 1300. 172 pp.

Ryan, K. C. 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fennica.* 36: 3-39.

Sarmiento, G. 1984. The Ecology of Neotropical Savannas. Harvard University Press, Mass. 235 pp + xii.

Schooley, H. 0., Hall, J. P. and W. Burry. 1979. Quantity of viable seed retained in old black spruce cones. Canadian Forestry Service, Bi-monthly Research Notes 35: 32.

Simard, M. and S. Payette. 2001. Black spruce decline triggered by spruce budworm at the southern limit of lichen woodland in eastern Canada. *Canadian Journal of Forest Research* 31: 2160-2172.

Sirois, L. 1993. Impact of fire on *Picea mariana* and *Pinus banksiana* seedlings in subarctic lichen woodlands. *Journal of Vegetation Science* 4 : 795-802.

Sirois, L. 1995. Initial phase of postfire forest regeneration in two lichen woodlands of northern Quebec. *Écoscience* 2: 177-183.

Sirois, L. and S. Payette. 1989. Post-fire black spruce establishment in subarctic and boreal Quebec. *Canadian Journal of Forest Research* 19: 1571-1580.

Sirois, L. and S. Payette. 1991. Reduced postfire tree regeneration along a boreal forest-forest-tundra transect in northern Quebec. *Ecology* 72: 619-627.

Sokal, R. and F. Rohlf. 1995. Biometry.3rd edition. W.H. Freeman and Company. New York. 997 pp.

Thomas, P. A. and R. W. Wein. 1984. The influence of shelter and the hypothetical effect of fire severity on the post-fire establishment of conifers from seed. *Canadian Journal of Forest Research* 15: 148-155.

Treter, U. 1995. Fire-induced succession of lichen-spruce woodland in Central Labrador-Ungava, Canada. *Phytocoenologia* 25: 161-183.

Tulk, K. A. 2004. Foraging ecology of red squirrels in Newfoundland: potential impacts on forest renewal. Unpublished MSc. Thesis. University of New Brunswick, Fredericton, New Brunswick. 115 pp + xiv.

Viereck, L. A. 1973. Wildfire in the taiga of Alaska. *Quaternary Research* 3: 465-495.

Viereck, L.A. and W. F. Johnston. 1990. *Picea mariana* (Mill.) B. S. P. Black Spruce *In* Burns, Russell M., and Barbara H. Honkala, tech. coords. 1990. Silvics of North America: 1. Conifers; Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC. vol.2, 877 pp.

Vincent, A. B. 1965. Black spruce: a review of its silvics, ecology and silviculture. Canadian Department of Forestry. Publ. 47-1100. 79 pp.

Wein, R. W. 1975. Vegetation recovery in arctic tundra and forest tundra after fire. Canadian Department. of Indian Affairs and Northern Development, ALUR Rep 74-75-62. 115 pp.

West, R.J. 1989. Cone depredations by the red squirrel in black spruce stands in Newfoundland: implications for commercial cone collection. *Canadian Journal of Forest Research* 19: 1207-1210.

Zasada, J.C., Viereck, L.A. and M.J. Foote. 1979. Black spruce seedfall and seedling establishment. *In* Ecological effects of the Wickersham Dome fire near Fairbanks Alaska. *Edited by* L.A. Viereck and C.T. Dyrness. US Forest Service, General Technical Report PNW-90. pp. 42-50.

Zhu, H. and A. U. Mallik. 1994. Interactions between Kalmia and black spruce: Isolation and identification of allelopathic compounds. *Journal of Chemical Ecology*, 20: 407-421.